The Mesozoic Chrysalidinidae (Foraminifera, Textulariacea) of the Middle East: the Redmond (Aramco) taxa and their relatives.

F. T. BANNER

Department of Palaeontology, British Museum (Natural History), Cromwell Road, London SW7 5BD, and
Department of Geological Sciences, University College London, Gower Street, London WC1E 6BT

M. D. SIMMONS

Exploration Technology Branch, BP Research Centre, Chertsey Road, Sunbury-on-Thames TW16 7LN

J. E. WHITTAKER

Department of Palaeontology, British Museum (Natural History), Cromwell Road, London SW7 5BD

CONTENTS

Synopsis. The seventeen Jurassic species of Textulariacea which had been named by Redmond (1965), placed by him in his new genera *Riyadhella* and *Pseudomarssonella*, and which had been used by Aramco for biostratigraphy in Saudi Arabia, have been redescribed and are re-illustrated. They are initially quadriserial, and may retain a simple, interiomarginal aperture; these include the terminally triserial *Riyadhella* emended and *Riyadhoides* nov.; or retain quadriseriality throughout ontogeny (*Redmondoides* nov.). The last of these contains *Redmondoides lugeoni* (Septfontaine) (*Valvulina lugeoni* Septfontaine) which is emended, for which metatypes are illustrated, and which is now recorded throughout Tethys. *Pseudomarssonella* is now restricted to initially quadriserial forms which gain areal, cribrate accessory apertures but still lack internal pillars. The acquisition of internal pillars characterizes *Paravalvulina* Septfontaine, a genus which ranges up into the earliest Cretaceous with *P. arabica* (Henson). Primary types and topotypes of this species (which was called *Dukhania arabica* by Henson) are also re-illustrated and redescribed. All these taxa are referred to the new subfamily Paravalvulininae.

The primary types and topotypes of *Dukhania conica* Henson are initially triserial and are referred to the subfamily Chrysalidininae Neagu; they are terminally biserial (unlike the terminally triserial *Chrysalidina* d'Orbigny, for which topotypes are illustrated) and have internal pillars, unlike the immediately ancestral *Praechrysalidina* Luperto Sinni, which is now also described from the Middle East. The Chrysalidininae are not older than Cretaceous.

Both the Paravalvulininae and the Chrysalidininae are referred to the Chrysalidinidae Neagu. They both contain specimens in which the micritic microgranules of the calcareous wall become aligned (the tests become 'protocanaliculate') and may even be canaliculate. The taxonomic significance of canaliculi is discussed and it is concluded that the development of canaliculation is gradational, from an initially random pattern of calcareous microgranules (in 'calc-agglutinated' walls), that the canaliculi might develop at various late ontogenetic stages (when their biological function became advantageous), and that their presence or absence cannot always be used to define supraspecific differences.

The probable phylogenetic histories of the Chrysalidininae and the Paravalvulininae, and the biostratigraphic value of their genera, are discussed.

INTRODUCTION

Detailed biostratigraphic studies in Saudi Arabia began in 1933, when Standard Oil of California was granted the first concession to explore for petroleum. After 1937, there was additional active participation by the Texas Oil Company, and, in 1944, the joint exploration company, once called 'California Arabian Standard', was renamed 'Aramco' (Arabian American Oil Company). Other companies joined, but from 1976 the Saudi Arabian governmental share-holding became 100%, and Aramco became a service company for the state, which was the holder of the world's largest national petroleum reserves. Many of the biggest oil-fields (Abqaiq, Abu Hadriya, Ghawar and many others) were found to have rich pay-zones in Jurassic rocks, and the Middle and Upper Jurassic biostratigraphy of Saudi Arabia became increasingly important, even in the early years of exploration.

As Redmond (1965) reported, 'a surprisingly large number of undescribed foraminiferal genera and species appear in the Middle and Upper Jurassic of Saudi Arabia'. Aramco agreed to release some of the material, and Redmond (1965) published descriptions of seventeen new 'ataxophragmiid' species, which he referred to his newly proposed genera *Pseudomarssonella* and *Riyadhella,* obtained from these rocks. The type specimens of these taxa were all solid, entire, and virtually matrix-free, and came from friable sediments sampled in water wells, stratigraphic wells or exploration wells drilled by Aramco, rarely from outcrops. As a result, strict topotypes could not be obtained by micropalaeontologists not associated with Aramco. Unfortunately, the original descriptions were accompanied only by small optical photomicrographs (all at × 50 magnification) in which many taxonomically important features (such as nature of the aperture, chamber arrangement, wall structure, etc.) were obscure. No thin sections of

any specimens were illustrated or even recorded, so internal structures, if any, were unknown. Also, it became very difficult, if not impossible, to compare these taxa with those found by other companies, elsewhere in the Middle East, in random thin sections of micritic limestones. Limestones such as these (e.g., the Araej, Musandam, Uweinat, etc.) constitute the mid and late Jurassic deposits in most of north-east coastal Arabia -- i.e. in Qatar, the United Arab Emirates, Oman, etc. Consequently, although Redmond's new taxa were used stratigraphically by Aramco (Redmond 1965, Powers 1968), they were not recorded publicly by workers in other oil companies.

Earlier, F. R. S. Henson and his associates (A. H. Smout, H. V. Dunnington and others), working on the Mesozoic rocks of Qatar, Iraq, Iran and Palestine, had recovered 'verneuilinids' from the early and mid Cretaceous which were referred to the new genus *Dukhania* (Henson, 1948). Redmond (1965) made no mention of these taxa, even though they had close morphological similarities to those which he had, himself, described; for example, they were microgranular, had 'agglutinating' walls, high spires, triseriality or quadriseriality, apertures which could become cribrate, etc. The species referred to *Dukhania* possessed internal pillars, but as no sections of *Pseudomarssonella* (in particular) had been prepared by Redmond, their morphological differences were not wholly clear.

In later years, Septfontaine (1977, 1981, 1988), after studying Mesozoic limestones (in thin section) from southern Europe and adjacent areas, published extensively on the morphology, taxonomy and possible phylogeny of high-spired 'valvulinids'. These included new taxa with extensive internal pillaring (e.g. *Paravalvulina*, reminiscent of *Dukhania*); this time, no isolated, entire specimens were known, and their morphology had to be deduced entirely from their (random) thin sections.

Luperto Sinni (1979), from the early Cretaceous of the

same region, described sections of her new microgranular, 'agglutinating' genus *Praechrysalidina*, which had no pillars but which did possess a high, triserial spire and an areal, cribrate aperture. For over a century, another, widely recorded triserial form, with a terminal, cribrate aperture but with internal pillars, had been the mid-Cretaceous *Chrysalidina* (d'Orbigny, 1839). A phylogenetic pattern was almost visible, but was far from clear.

A similar lack of clarity beset the Jurassic taxa which lacked cribrate apertures and which often had unknown internal structures. While *Riyadhella* (and perhaps some *Pseudomarssonella*) had simple, interiomarginal apertures, this was also believed to characterize the quadriserial-triserial *Eomarssonella* (Levina, 1972), known as solid specimens from the late Jurassic of western Siberia, and the 'triserial' '*Valvulina lugeoni*' (Septfontaine, 1977), known only as random thin sections from the late Middle Jurassic limestones of southern Europe. There were several other published taxa; all were of Jurassic–Cretaceous age and had distinct morphological resemblances.

In an attempt to clarify their descriptions, review their systematics, revise their nomenclature, explain their phylogeny and determine their value in biostratigraphy, the collections of primary types of the taxa published by Redmond (1965) and by Henson (1948) have been restudied. Where possible, paratypes of species of *Riyadhella* and *Pseudomarssonella* have been thin-sectioned, so that the internal structure of these taxa is now known. Topotypic thin sections of limestones with '*Valvulina' lugeoni* have also been studied. The information from the primary types of *Dukhania* and related taxa has been supplemented by that obtainable from other, previously unpublished specimens (including topotypes) in the Henson and associates collection, deposited in the British Museum (Natural History). Specimens collected from Oman (Simmons & Hart 1987, Smith *et al*. 1990) and from the United Arab Emirates (BP Exploration and the Abu Dhabi National Oil Company) have also yielded much information.

SPECIMEN DEPOSITORIES AND STUDY METHODS

The Redmond Collection of Aramco specimens is deposited in the American Museum of Natural History (Department of Fossil Invertebrates), New York, USA (abbreviated to AMNH in this paper). The holotype specimens of each taxon are individually numbered, but the paratype specimens of each taxon are curated together, being mounted in a single paratype slide for each taxon, and bear a common number; these paratypes have been distinguished, for illustration in this paper, by a letter appended to the curation number. Both holotypes and paratypes bear curation numbers which are prefixed 'FT-'; thus, a particular paratype may be labelled here as 'AMNH FT-1234A'.

The Redmond specimens which were not sectioned were imaged by the ISI 60A scanning electron microscope (SEM), using the Environmental Chamber and back-scattered electrons; they have not been coated in any way. The paratypes which were sectioned were first imaged by the Hitachi 2500 SEM, using secondary electrons, and were coated with gold-palladium.

All specimens which are deposited in the British Museum (Natural History), Department of Palaeontology, London (abbreviated to BMNH in this paper) are registered by numbers prefixed 'P'.

THE NATURE OF THE TEST WALL

The nature of the composition and structure of the walls of so-called 'agglutinated' foraminifera has recently been discussed by Bender (1989) and by Loeblich & Tappan (1989), amongst others, and the views expressed in these papers have been taken into account here; in particular, the former has published some illuminating SEM imagery. However, it is necessary to redefine the terms which will be used here and to explain, albeit briefly, the reasons for these redefinitions.

All the taxa redescribed in this paper possess walls which are dominantly or wholly calcareous (calcitic), which may or may not possess canaliculi (as discussed below) and which may or may not contain clearly inorganic, mineral fragments (such as fine silt quartz grains). In spite of the differences which can occur between them (such as, for example, the presence or absence of silt quartz), they are obviously all essentially the same: none has the characters which would lead to their recognition as being walls of Rotaliina, for example. We explain below how they are all easily recognizable as belonging to members of the Textulariina.

The walls of the Textulariina may be constructed of inorganic (originally terrigenous) grains, glued together by organic (mucopolysaccharide?) cements. Such walls occur particularly in benthonic species which inhabit (or inhabited) oceanic waters below the calcium carbonate compensation depth, or marsh environments of low pH, or other habitats where solid calcium carbonate could not survive. Elsewhere, the organic cements could be supplemented by secretion of calcium carbonate; analogously to the 'dry-stone walling' technique of humans, the gaps between the terrigenous mineral grains of the walls could be filled with packed microgranules of calcite. This calcite retains its microgranular form when viewed by SEM, showing that the microgranules are, themselves, coated with ultramicroscopically thin organic laminae – if they were not, the form of the microgranules would have been lost, and the calcite would have been visible as a continuous, undivided mass. The organic cements may be constructed of fibres, nets, 'foam' or sheets, or combinations of these (Fig. 1a). They 'glue' the terrigenous grains or calcitic microgranules together, to make a coherent, continuously structured wall; the term 'agglutinated' (from *glutinare*, to glue) is appropriate, whether the calcitic microgranules were secreted by the foraminifer or not; the term 'arenaceous' is most inappropriate, as no 'sand' grains may be involved. In fact, no inorganic grains of terrigenous, mineral origin may be present at all.

Some textularine taxa may have walls wholly composed of microgranules of calcite, agglutinated together (Bender 1989: pl. 8). These are 'agglutinating' but they are certainly not 'arenaceous'. These calcite microgranules may be arranged randomly in the walls, or they may be agglutinated into parallel rows, virtually or wholly perpendicular to the wall surface (Fig. 1b). In neither case is there any alignment of the optical axes (the 'c-axes') of the calcite microgranules; in thin section, the wall may have its more transparent
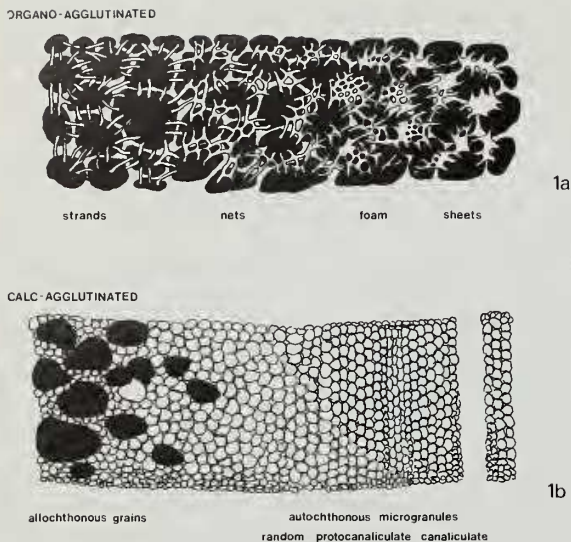
ORGANO-AGGLUTINATED

strands   nets   foam   sheets

1a

CALC-AGGLUTINATED

1b

allochthonous grains   autochthonous microgranules
                        random protocanaliculate canaliculate

Fig. 1 The wall structures of members of the Textulariina: the black grains represent non-calcareous particles of rocks or minerals, while the white microgranules represent calcareous (calcite or aragonite) autochthonous particles.

a, the forms of *organo-agglutinated* cements: separate organic *strands* become joined to form *nets*, and these nets infill to form porous *'foam'* or non-porous *sheets*.

b, in *calc-agglutinated* tests, allochthonous foreign grains may be cemented together by calcareous *microgranules*; these autochthonous microgranules may remain randomly arranged but may build the wall in the absence of foreign, allochthonous grains; when the microgranules become arranged in parallel rows, perpendicular to the wall surface, the wall becomes *protocanaliculate*; canaliculi can develop between these parallel stacks of microgranules, so that the wall becomes *canaliculate*.

(lighter-coloured) zones, where the microgranules are larger, or its darker, less translucent zones, where the microgranules are smaller, but in no case has the wall a 'fibrous', 'glassy' or 'hyaline', rotaline appearance. In the latter, the optical axes of the aligned microgranules are themselves aligned, so that the parallel rows of microgranules, with their equally parallel c-axes, look like fibrous crystals when seen through an optical microscope. If the c-axes are orientated perpendicular to the wall surface, such 'hyaline' walls have been called 'radial', but if the c-axes of groups of aligned microgranules are oblique to the wall surface, with different directions of obliquity, then they have been called 'granular' (Loeblich & Tappan 1964: C94–95). This latter term was a reference to the optically 'granular' or 'speckled appearance of the surface ... in polarized light, owing to different grain orientations and resultant differences of refractive index. Some ... forms may even appear granular in reflected light ...'. (Loeblich & Tappan, *loc. cit.*). It is now clear that the use of the term 'granular' for this optically speckled appearance (e.g., as in Loeblich & Tappan, 1988: 615) must be abandoned for the sake of the consistently meaningful, morphological usage of the names 'granule' and 'microgranule'. All the forms of wall discussed above are morphologically microgranular when viewed by SEM; granules of minerals may be agglutinated into walls which have no optical, c-axis linearity. So we suggest that 'microgranules' be used to label grains which can only be distinguished by electron microscopy (e.g., by SEM),

while 'granules' be reserved for grains which can be distinguished by optical microscopy.

Also, we suggest that the *agglutinated* taxa, in which the optical axes of constituent microgranular and/or granular minerals are randomly orientated and are not regularly aligned, may include

(a) taxa with organic cements only (these organic cements may, themselves, be fibrous, laminar or microgranular), and are *'organo-agglutinated'* (Fig. 1a);

(b) taxa with additional ferric or other non-calcareous microgranular cements (e.g. *'ferro-agglutinated'*);

(c) taxa with additional calcareous material (i.e. *'calc-agglutinated'*), maintained as microgranules by ultramicroscopic organic membranes; these calcareous microgranules may (as in the categories above) also agglutinate allochthonous grains of other minerals (e.g., quartz); also, the microgranules may be randomly packed or agglutinated into parallel rows, usually perpendicularly to the wall surface (Fig. 1b).

All of these categories belong to the Textulariina Delage & Hérouard, 1896 (see Loeblich & Tappan, 1988).

All the taxa in the Redmond, Henson and other collections described in this paper have walls in category (c); all are *calc-agglutinated microgranular*. Additionally, some may also agglutinate quartz granules, and some may be partly canaliculate. The significance of the latter is discussed below.

THE SIGNIFICANCE OF CANALICULI IN TAXONOMY

Canaliculi in classification

The presence or absence of canaliculi, in the walls of Textulariina with calcitic cement, has been used by Loeblich & Tappan (1988, 1989) as a morphocharacter to define the difference between superfamilies (e.g., canaliculate Textulariacea, noncanaliculate Verneuilinacea). However, it had already been pointed out (e.g., by Banner & Desai 1985, Desai & Banner 1987) that canaliculi evolved independently in different lineages, at different times in the Mesozoic and Palaeogene, and that the superfamilies could not be distinguished on one morphocharacter alone. Even some genera (e.g., canaliculate *Dorothia* developing from ancestral, noncanaliculate *Praedorothia*) could evolve more than once. The canaliculate descendants are superficially so similar to their noncanaliculate ancestors that they are generically indistinguishable unless they are sectioned, or broken and viewed with SEM; any useful classification would group them together, so that their identity could be immediately compared. To separate into different superfamilies the members of such closely related pairs of genera as *Praedorothia – Dorothia*, *Protomarssonella – Marssonella*, *Textulariopsis – Textularia*, *Pseudoclavulina – Clavulinopsis*, *Verneuilina – Hemlebenia*, *Gaudryina – Connemarella*, etc, when the different pairs are not closely related to the other pairs, would produce a suprageneric classification which would be misleading both phylogenetically and taxonomically. Clearly, for example, *Praedorothia* and *Dorothia*, both of which secrete calcitic cement, have the same coiling and growth modes, and the same apertural, test and chamber shapes, should be referred to the same superfamily (maybe even to the same family),

even though one is canaliculate and one is not. One directly and repeatedly evolved from the other. Forms which are intermediate in this evolution, and in which the canaliculation of the wall was partial or indistinct, would produce great problems of classification if the supraspecific characters were to be artifically elevated into major, suprageneric ones.

Tubule-containing and canaliculate walls

Even when there is no known evolutionary transition from one category into another, lack of careful distinction of the nature of a textulariid wall can lead to confusion. An example is *Spirorutilis wrighti* (Silvestri). Banner & Pereira (1981), in their study of canaliculation in the textulariids, believed *S. wrighti* to have solid walls, and referred it to the solid-walled Spiroplectamminidae (in contrast to the canaliculate Textulariidae). Their SEM photographs of this species, and of its wall, were reproduced by Loeblich & Tappan (1988: pl. 120), who used its supposed senior generic synonym *Spiroplectinella* and placed it in the solid-walled Superfamily Spiroplectamminacea (1988: 110–112), far from the canaliculate Superfamily Textulariacea (1988: 168). This was followed by Hottinger *et al.* (1990). However, Bender (1989: 298; pl. 10, fig. 1; pl. 16, fig. 25) has shown that specimens of '*Spirorutilis*' *wrighti* have walls which are far from solid, even though she still places them in the Superfamily Spiroplectamminacea. She distinguishes (1989: 277) three types of 'porensysteme' within those textulariids which use calcite cement: the 'anastomosierende' (anastomosing, irregularly shaped, but often narrow and characteristically tubular) spaces in the walls of, e.g., *S. wrighti* (the type species of *Spiroplectinella* Kisel'man), and now also shown to be present in the walls of '*Textularia*' *carinata* d'Orbigny (the type species of *Spirorutilis* Hofker) by Hottinger *et al.* (1990); the 'geradlinig unverzweigt' (rectilinear, unbranched) canaliculi of *Textularia* spp.; and the 'distal verzweigt' (distally branched) canaliculi of *Valvulina*, *Clavulina* spp. and '*Gaudryina*' *rudis* (Wright), the last species used, because of its canaliculation, to typify the new genus *Connemarella* of the Textulariacea by Loeblich & Tappan, 1989. Clearly, distinction must be made between taxa which have walls with anastomosing, irregular tubules and those which have true, regular, subparallel canaliculi, even though the walls of neither are truly solid. The tubules are not known to evolve into canaliculi; the latter seem to have their origin in truly solid, calcitic walls in which the constituent granules become regularly aligned.

Protocanaliculate walls

It has been shown that in some species not known to have had canaliculi, the calcareous granules of their walls could become aligned in a way which would allow canaliculation readily to develop. The latter would have been able to develop 'between these vertical parallel stacks of granules' (Banner & Desai, 1985: 87, regarding *Verneuilina tricarinata* d'Orbigny, their pl. 3, figs 7, 8). We can term these calcitic, solid-walled species, in which the constituent granules are aligned in parallel rows perpendicular to the wall surface, 'proto-canaliculate'.

However, fully canaliculate species (even wholly calcareous ones) often do not readily show such alignment of granules even when the canaliculi, themselves, are prominent (e.g., *Valvulina oviedoiana* d'Orbigny, as figured by Banner & Pereira, 1981: pl. 9, figs 1–3, 8), but such alignment may,

nevertheless, be present. Bender & Hemleben (1988) showed not only that the calcitic cement of *V. oviedoiana* was biologically secreted but that in it, also, the granules ('individual crystals') of calcite were aligned into granular rods (1988: pl. 1, figs 4, 6, 7), and that the granules and their rod-like assemblages were coated with 'organic envelopes' (1988: pl. 1, fig. 5). The rod-like parallel stacks of granules could themselves be grouped parallel to each other, to produce 'packets' of granules in parallel rows (Bender 1989: 276). These 'packets' of 'rods' of aligned calcitic granules, as seen between the canaliculi in Holocene *V. oviedoiana*, closely resemble those observed in some Cretaceous taxa (e.g., *Dorothia pupa* (Reuss), as figured by Desai & Banner, 1987: pl. 1, figs 2c, 2d).

The walls of some Mesozoic taxa (e.g., *Marssonella oxycona* (Reuss), as figured by Desai & Banner, 1985: pl. 3) have fibrous units of calcite aligned parallel to each other, and parallel to the canaliculi which are present between large groups of them. These fibrous units show no sign of granular composition, and they do not seem to be grouped into 'packets'. The canaliculi of *Marssonella* are separated by far greater numbers of fibrous units than the smaller numbers of granular 'rods' which constitute the walls between the canaliculi of *Dorothia* (see, e.g., Desai & Banner, 1985: pls 1–3). Such differences of structure may prove to be characteristic of different genera and separate evolutionary lineages, but more research must yet be undertaken.

Nevertheless, it seems clear that alignment of the primary calcitic constituent granules of the walls was necessary prior to the development of canaliculi. It has been assumed (e.g., by Banner & Desai, 1985) that such alignment may characterize species but cannot be used to distinguish supraspecific groups, in contrast to the presence of canaliculi, which can be used for such distinction; indeed, as noted above, Loeblich & Tappan (1988) used them to distinguish groups as important as superfamilies.

The ontogenetic appearance of canaliculi

Although it has never been explicit, the assumption has been made that such alignment of wall structures was constant throughout the ontogeny of the species concerned – that such alignment of primary calcitic granules or the presence of canaliculi appeared at a given stage of evolution, and thereafter occurred uniformly from nepionic to ephebic (and maybe even gerontic) growth stages. Certainly, in some figured taxa, canaliculi are uniformly present in the chamber walls throughout test growth; examples include Recent *Textularia agglutinans* d'Orbigny (e.g. Banner & Pereira, 1981: pl. 1, fig. 6) and Cretaceous *Dorothia pupa* (Reuss) (Desai & Banner, 1987: pl. 1, fig. 2b). The possibility that, in other taxa, there were ontogenetically late appearances and development of canaliculi was not considered.

The speed of evolution of canaliculi

The apparent uniformity of the appearance and development of canaliculation in the walls of some taxa could have resulted from the rapid evolution of canaliculi during the phylogeny; it could have been that canaliculi first developed in late ontogenetic stages, and later spread to earlier ones, but that in the fossil record this 'ontogenetic spread' is hidden by the rapidity of the evolution as a whole. The evolution would appear to have been 'punctuated', as in the phylogenetic appearance of

the Textulariidae (as redefined by Banner & Pereira, 1981) or of true *Marssonella* (Desai & Banner 1987). In such cases, the presence or absence of canaliculi provide clear, biostratigraphically useful, supraspecific taxonomic distinctions.

In other cases (e.g., the *Chrysalidina* evolution studied here), the evolutionary acquisition of canaliculation was much slower, more 'gradual'. The late ontogenetic development of canaliculi was not hidden in an abbreviated fossil record. The development of canaliculi during test growth could have been entirely related to the acquisition of individual ontogenetic maturity, possibly under particular micro-environmental conditions, and was not acquired by all specimens at all of their growth stages, at a recognizable evolutionary point in their phylogenetic lineage – or even at identical ontogenetic points. In these cases, the presence or absence of canaliculi cannot be used for supraspecific taxonomic distinction, and cannot even be used, independently, to distinguish between species.

This exemplifies the rule which applies in the study of all groups of foraminifera: a particular morphocharacter may be of taxonomic importance and biostratigraphic usefulness in one group, but may be of little taxonomic utility and of limited biostratigraphic value in another, even closely related, group.

Canaliculi, keriothecae and alveolae

The variable taxonomic importance of the development of canaliculi has been accepted by, e.g., Septfontaine (1988), who diagnosed his concepts of the Mesoendothyridae as always possessing a 'keriotheca', the Hauraniidae in lacking it (but possessing a 'hypodermal network'), and the Valvulinidae as sometimes possessing it. The closely spaced and parallel canaliculi of many Lituolacea (e.g., in Mesozoic *Lituosepta* of the Mesoendothyridae (*sensu* Septfontaine, 1988; Orbitopsellidae *sensu* Loeblich & Tappan, 1988) and Cenozoic *Valvulina* of the Valvulinidae) produce a wall structure which morphologically closely resembles the keriotheca of many Palaeozoic fusulinids (e.g., the Schwagerinidae). When the canaliculi are thin-walled and very closely spaced, as in the paratype *Dukhania conica* Henson (Fig. 25a, p. 114), the resemblance to a schwagerine keriotheca is very strong. They may well have had an analogous biological function, but there can be no doubt that the structures were evolved independently, and have different taxonomic and biostratigraphic value in different foraminiferal groups.

Thicker-walled, more widely spaced canaliculi have strong resemblance to the structures called 'alveoli' in lituolids such as *Alveosepta*, *Buccicrenata*, *Alveocyclammina*, etc. (see illustrations in Loeblich & Tappan, 1988); these narrow hypodermal alveoli may branch, but, as Bender (1989, see above) has pointed out, so can the canaliculi of *Valvulina*, *Clavulina*, etc. (see, for example, the bifurcating canaliculi of *V. oviedoiana* d'Orbigny, figured by Banner & Pereira, 1981: pl. 9). The only morphological distinction between such broad canaliculi and narrow alveoli seems to be the internal closure of the former by pustulae of the inner organic lining of the wall (illustrated by transmission electron microscopy in Bender, 1989: pl. 10, figs 3–5), which are sometimes calcified and preserved even in fossils (illustrated by SEM in Banner & Pereira, 1981: pl. 6, fig. 6; pl. 8, fig. 8; pl. 9, fig. 11).

Again, there may well have been analogous biological functions for both structures. It has been suggested that the narrow hypodermal alveoles of *Alveosepta*, etc., which appear to have evolved in conditions of reduced illumination,

could have allowed ionic exchange between internal cytoplasm and surrounding sea-water, through the extremely thin epidermis (Banner & Whittaker 1991); the canaliculi of the textulariids probably had, and probably still has, a similar function. This contrasts with the broad hypodermal alveoles of lituolids which inhabited very shallow, tropical water (e.g., *Pseudocyclammina lituus*); such species may have used the environmental irradiance for photosymbionts in the alveoli, a function which canaliculi could not have had (Banner & Whittaker 1991).

Summary and conclusions

The development of canaliculi during phylogenesis seems to have been to the biological advantage of the evolving taxa; they may well have aided the organism directly but subtly to control its cationic concentration. Canaliculi independently appeared in several lineages, and once gained they were never lost; there is no example of their evolutionary disappearance.

Canaliculi, narrow hypodermal alveoli and schwagerinid keriothecae could all have had analogous biological functions. However, they cannot be proved to be homologous; they certainly evolved quite independently. Morphological extremes of each are clearly distinguishable (the morphological similarities between the other extremes can be confused but do not indicate their identity), and they should be given separate names and definitions. Essentially, the keriotheca is a uniform mass of favosely arranged, parallel, narrow tubules, each thin-walled and much longer than it is broad, and all are closely appressed; the chamber wall (the keriotheca) *consists* of these tubules. In contrast, canaliculi penetrate the microgranular chamber wall, are not closely appressed, and are independently sealed by pustules of the inner organic lining. Alveoles are similarly spaced but have no such inner seal, and can be almost as broad as they are long (especially in lituolids with thin chamber walls).

Canaliculi appeared relatively abruptly in the evolution of some lineages but slowly in others. Even the protocanaliculate evolutionary stages can be recognized to have appeared slowly and independently. When canaliculi evolved slowly, they can be seen to have first appeared in the last growth stages of the tests. It was probably in that phase of life, when the test was largest, that the canaliculi were most useful in providing means (additional to those in the extruded pseudopodia) for the intracameral cytoplasm to communicate biochemically with exterior seawater. When species, such as those of *Dukhania* and *Chrysalidina*, develop with canaliculi only in the last chambers of some specimens, the use of canaliculi to define suprageneric differences (such as those between families and superfamilies) becomes impossible. It is unwise to attempt it even when the evolutionary acquisition of canaliculi is relatively abrupt, as it is then misleading both taxonomically and phylogenetically.

SYSTEMATIC PALAEONTOLOGY

Superfamily **TEXTULARIACEA** Ehrenberg, 1838
Family **CHRYSALIDINIDAE** Neagu, 1968

DIAGNOSIS EMENDED. Wall microgranular, agglutinating, calcareous, with relatively small amounts (if any) of agglutinated,

noncalcareous grains, and solid (sometimes protocanaliculate) or canaliculate, or both; test high trochospiral, with quinqueserial or quadriserial or triserial or biserial coiling modes, or with certain consecutive pairs of these; the primary aperture is interiomarginal and centred about the long axis of coiling; in terminally quadriserial or quinqueserial forms, an umbilicus is present and the aperture is covered with a broad intraumbilical flap; the umbilical flap may be penetrated by areal, multiple, pore-like, accessory apertures, and internal pillars may develop between successive intraumbilical flaps.

REMARKS. This family is divisible into two subfamilies, which contain genera which may be morphologically very similar (Dukhania of the Chrysalidininae, Paravalvulina of the Paravalvulininae) but which have different origins and give ultimate rise to morphologically very different forms. The Cretaceous Chrysalidininae are essentially triserial, initially at least; they evolve as a single lineage, developing umbilically pillared genera which are, successively, terminally biserial, then triserial and ultimately quadriserial (or even multiserial), as the internal zone of pillaring became increasingly broad. In contrast, the mainly Jurassic Paravalvulininae (Bajocian–Kimmeridgian, surviving into the Valanginian and possibly the Hauterivian), are quinqueserial and/or quadriserial, or both, evolving forms which are terminally triserial; these may be very slender (some species of *Riyadhoides* and *Riyadhella*) or broadly conical and internally pillared (*Paravalvulina*).

Subfamily CHRYSALIDININAE Neagu, *nom. transl.*

DIAGNOSIS. Test triserial throughout ontogeny (at least in the megalospheric generation) or becoming biserial or quadriserial in the adult.

KEY TO GENERA INCLUDED

1. Triserial throughout, no internal pillars: *Praechrysalidina* Luperto Sinni, 1979 (Hauterivian?–Barremian–Albian)
2. Initially triserial (in megalospheric form), with internal pillars:
   2.1. Biserial in adult:
      2.1.1. Septa convex:
         2.1.1.1. Chambers relatively low, septa at broad angles to long axis of test: *Dukhania* Henson, 1948 (Aptian/Albian?–Cenomanian)
         2.1.1.2. Chambers relatively high, septa oblique to long axis of test: *Pseudochrysalidina* Cole, 1941 (Eocene)
      2.1.2. Septa plano-concave: *Vacuovalvulina* Hofker, 1966 (Palaeocene)
   2.2. Triserial in adult: *Chrysalidina* d'Orbigny, 1839 (Aptian?–Cenomanian)
   2.3. Quadriserial (or multiserial) in adult: *Accordiella* Farinacci, 1962 (Coniacian–Santonian)

REMARKS. *Vacuovalvulina* must have arisen independently from the phylogeny described below, probably evolving from canaliculate, true *Marssonella* at or near the Cretaceous–Palaeogene boundary, but its evolution is not yet demonstrable; if this supposition is correct, then *Vacuovalvulina* does not belong to the Chrysalidininae as here understood.

Pseudochrysalidina may also ultimately be removed from this subfamily, as it may have evolved directly from *Valvulina* but this, also, has yet to be demonstrated.

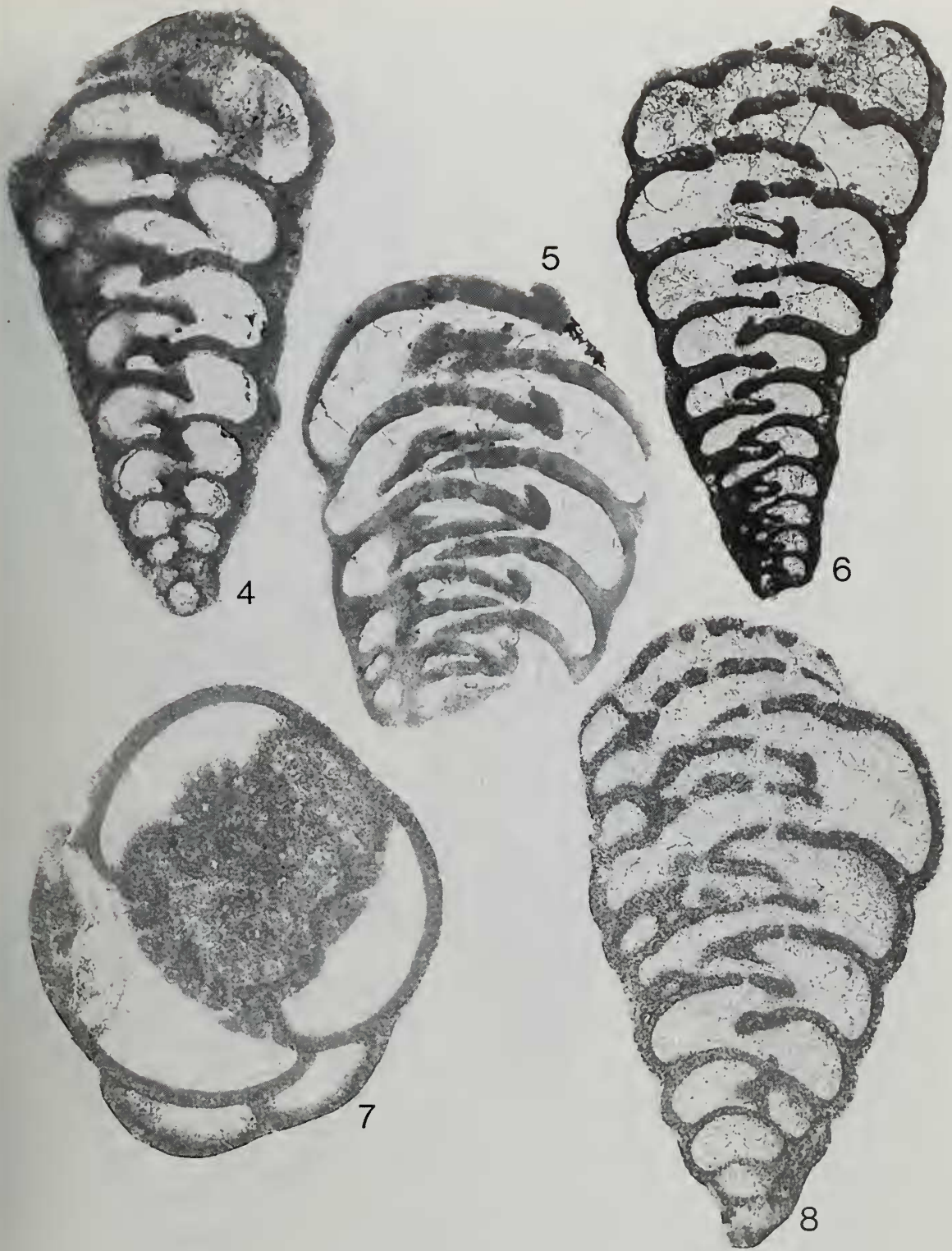### Genus *PRAECHRYSALIDINA* Luperto Sinni, 1979

TYPE SPECIES. *Praechrysalidina infracretacea* Luperto Sinni, 1979 (see Figs 2–8).

REMARKS. In his synoptic, comprehensive study of Mesozoic neritic foraminifera, Septfontaine (1981: 184, 188) noted the appearance, in the early Cretaceous, of 'Valvulines spéciales' which he believed were descended from 'Valvulina' lugeoni by developing modification to the 'dent valvulaire' analogous to that later displayed by *Chrysalidina*; he figured a random thin section of this form, showing its characteristic multiple, pore-like, areal apertures, from Lower Cretaceous limestone of Turkey (1981: pl. 2, fig. 12). Earlier, Gušić (1975: 26; pl.4) had figured the same species, from the 'Uppermost Aptian – Lowermost Albian' of Mt Medvednica, northern Croatia, Yugoslavia, as '*Chrysalidina* cf. *gradata* d'Orbigny'; he noted that this form lacked the pillars and buttresses of true, Cenomanian *Chrysalidina*, and should be distinguished. Both of these authors clearly recognized the affinity of these early Cretaceous forms to the late Cretaceous genus, and believed that they deserved recognition. In 1979, Luperto Sinni described and named it, using thin sections of specimens (from the limestone of the terminal part of the early Aptian of western Italy) as the primary types. Later (*in* Schroeder & Neumann 1985: 22) she recorded it also from the late Aptian and late Albian, and from localities as far afield as Somalia, suggesting that it might form part of an evolutionary lineage '*Valvulina*' *lugeoni* → *Praechrysalidina cretacea* → *Chrysalidina gradata* → '*Chrysalidina*' (*vel Pseudochrysalidina*) *floridana*.

We believe that this phylogenetic theory must be modified. There is no evidence to link *Praechrysalidina infracretacea* with '*Valvulina*' *lugeoni* (here placed in *Redmondoides* n. gen., p. 125), and there is a considerable stratigraphic gap between them. Also, *P. infracretacea* is, like its descendants, initially triserial. We would refer it to the subfamily Chrysalidininae, separate and distinct from the stratigraphically earlier, fundamentally quadriserial Paravalvulininae. The stratigraphically oldest known occurrences of *P. infracretacea* are those recorded by Simmons & Hart (1987) from the Habshan Formation (probably Valanginian) of Oman. We suspect that *Praechrysalidina* arose quickly but directly from *Verneuilinoides* sp., in the earliest Cretaceous, by the opening of the umbilicus and the acquisition of broad apertural flaps, which rapidly became penetrated by accessory, areal, cribrate, pore-like apertures. In ontogeny, the interiomarginal primary aperture remained open in the nepionic growth stage, but in neanic growth this became covered by the perforated, broad, apertural plate-like flaps, while the accessory interiomarginal aperture still remained. By the ephebic stage of development, the flaps became fused to the terminal faces of juxtaposed chambers, and the accessory interiomarginal apertures became sealed. Only the areal accessory apertures remained open to allow the internal cytoplasm access to the exterior of the test. The primary interiomarginal apertures, now wholly internal, became high and wide, and occupied the whole height of what was once the apertural faces of the chambers. Consequently, the apertural flaps became convexly inflated (Figs 4–8), producing a convex termination to the tests (Figs 2–3), heralding the evolution of the succeeding *Dukhania* and *Chrysalidina*. The juxtaposed chambers separated in their axio-medial areas, and a true umbilicus developed, always covered by the apertural flaps.
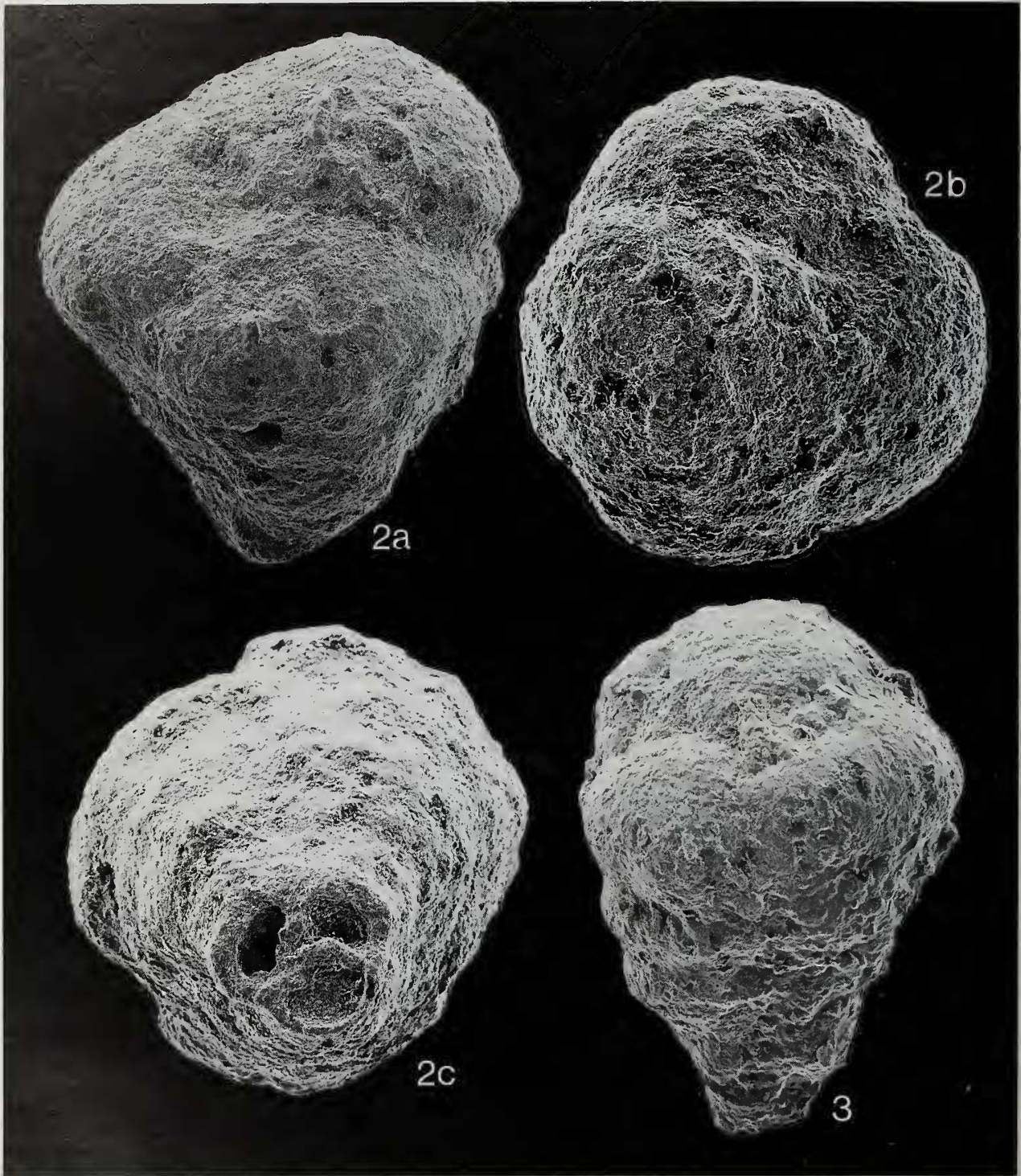
Figs 2–3 *Praechrysalidina infracretacea* Luperto Sinni. Figs 2a–c, BMNH P 52580, from Qatar, well Dukhan-2, 4375–4380 ft depth, Hauterivian. a, axial view (length 1320 μm), × 70. b, terminal view, × 70. c, initial view, showing triseriality, × 70. Fig. 3, BMNH P 52581, from United Arab Emirates, well Umm Shaif-2, Upper Shuaiba Formation, Aptian; axial view (length 1180 μm), × 80.

gs 4–8 *Praechrysalidina infracretacea* Luperto Sinni. Fig. 4, BMNH P 52582, from United Arab Emirates, well Umm Shaif-2, Upper Shuaiba
Formation, Aptian; axial section (length 1000 μm), × 110. Fig. 5, BMNH P 52583, from Qatar, well Dukhan-23, 3710–3720 ft depth, Aptian;
axial section (length 1010 μm), × 80. Fig. 6, BMNH P 52584, from United Arab Emirates, well Umm Shaif-2, Upper Shuaiba Formation,
Aptian; axial section (length 2320 μm), × 45. Fig. 7, BMNH P 52585, from northern Iraq, Mosul region, well Mushorah-1, 7005–7010 ft
depth, Qamchuqa Formation, Albian; equatorial section (breadth 1960 μm), × 45. Fig. 8, BMNH P 52586, from Oman, sample IT 86 908,
Aptian; axial section (length 1760 μm), × 65.

The walls of the chambers often became protocanaliculate and then sometimes (but not always) canaliculate in the latest growth stages; this was illustrated by Luperto Sinni (*in* Schroeder & Neumann, 1985: pl. 6, fig. 10) for one topotype *P. infracretacea*, but other specimens (e.g., Figs 4–6) have walls which remain solid.

Praechrysalidina infracretacea Luperto Sinni was known to Henson and his associates, in the Iraq Petroleum Company, as '*Pseudochrysalidina* MC/2' ('MC' probably being a record of its first recognition by Max Chatton). It occurs in the Hauterivian of well Dukhan-2, Qatar (Figs 2a–c) and was recognized by them to occur in the Aptian of Dukhan well 23, Qatar (Fig. 5), and in the Albian–Barremian Qamchuqa Limestone Formation of northern Iraq (e.g. in well Mushorah-, at 7005–7010 ft to 7560–7565 ft depth) (Fig. 7). We have also recognized it in the Aptian drilled off-shore in the United Arab Emirates (Figs 3, 4, 6) and outcropping in Oman (Fig. 8).

The evolution from *Praechrysalidina* into *Dukhania* was gradational and continuous (Figs 13, 14, 15). The umbilicus and the covering flaps broadened, and structurally supportive pillars developed between successive flaps. The pillars appear to have arisen from the outer, distal surfaces of later flaps, extending to approach, and then reach, the ventral surfaces of succeeding flaps (Fig. 14). This is opposite to the way in which the inter-flap pillars seem to arise in *Paravalvulina* (p. 140). Also, the evolution into *Dukhania* was marked by a broadening of the test, which tapered more rapidly (Figs 13–15), and the developments of terminal biseriality. This was independent of, and distinct from, the evolution of *Praechrysalidina* into *Chrysalidina* (Figs 9–12), when the slender, slowly tapering test and terminal triseriality were retained, even though interflap pillars were also developed.

Genus *DUKHANIA* Henson, 1948

TYPE SPECIES. *Dukhania conica* Henson, 1948.

DIAGNOSIS EMENDED. A chrysalidinid with (megalospheric) triserial coiling reducing to adult biseriality; in each chamber of each adult whorl, the primary, interiomarginal aperture is covered by a broad flap which is penetrated by multiple, areal, accessory pore-like apertures; internal pillars develop between successive apertural flaps; wall solid, sometimes becoming protocanaliculate, sometimes (but not always) becoming canaliculate in the last-formed chambers.

Dukhania conica Henson, 1948   Figs 17–26

1948 *Dukhania conica* Henson: 615; pl. 15, figs 2, 4, 5, 8; pl. 17, figs 2, 3.

DESCRIPTION EMENDED. Test calcareous, microgranular; nepionic and neanic chamber-walls may be imperforate and non-

canaliculate, but, in some specimens, ephebic and even neanic chambers may have walls which become protocanaliculate and even canaliculate. The innermost and outermost surfaces of both walls and septa consist of relatively much smaller microgranules, and appear darker when seen in thin section; the innermost layer, at least, can be perforated by canaliculi when they are developed. The test-form is conical. The megalospheric test is initially triserial (the microspheric test being initially quinqueserial), becoming biserial in a late ontogenetic stage. The nepionic–ephebic primary aperture is simple, umbilical and interiomarginal, rapidly acquiring the additional, neanic–ephebic, multiple, cribrate, areal, accessory pore-like apertures which are situated in the increasingly convex and broad apertural flaps (the 'trematophore-like', 'central shield' of Henson, 1948); both apertural flaps of the last-formed chambers join medially, with a closed suture, and have a convexity distinct from that of the terminal faces of the last chambers which remain exposed marginally. Internally, pillars develop between the apertural flaps, producing a labyrinthic area central to the long axis of the test; the volumes of the chambers themselves, marginal to the flaps, lack pillars.

REMARKS. Henson (1949) stated that *Dukhania* should be considered a synonym of *Pseudochrysalidina* Cole; for this reason, many of the specimens of *D. conica* in the Henson and associates collection were re-labelled, by them, to read '*Pseudochrysalidina conica*'. We accept Henson's earlier view, and consider *Dukhania* to be phylogenetically and morphologically distinct.

DIFFERENTIATION. *Dukhania* differs from *Paravalvulina* in its triserial–biserial coiling mode. Also, the apertural flaps ('shields') of *Dukhania*, even in the earliest whorls, have a strongly convex curvature very similar to that of the true, intercameral septa (and, of course, the terminal faces of the last chambers); in *Paravalvulina* spp. (from Middle Jurassic to ?Hauterivian) the 'shields' are flattened or only slightly convex. *Dukhania* differs from *Chrysalidina* in its terminal biseriality, developed even though its test is much less elongate; both genera may develop canaliculi in some ontogenetically late chamber walls, but retain solid walls throughout much of their tests.

AFFINITY. The initial triseriality of the test, with possession in the earliest whorls of very convex, cribrate apertural 'shields' (apertural-umbilical flaps), shows the affinity of *Dukhania* to its ancestral *Praechrysalidina*. Specimens which possess all the characters of *P. infracretacea* in their early whorls begin to develop a few, heavy pillars between successive apertural flaps of the last-formed chambers (Figs 13, 17) and are morphologically intermediate between *P. infracretacea* and the descendant *D. conica* (see p. 115). The development of canaliculation only occurs in the walls of the largest specimens of *D. conica*, but it may be observed more clearly and

Figs 9–12 Morphologically intermediate forms between *Praechrysalidina infracretacea* Luperto Sinni and *Chrysalidina gradata* d'Orbigny. Fig. 9, BMNH P 52587, from northern Iraq, Mosul region, well Mushorah-1, 7560–7565 ft depth, Qamchuqa Formation, Albian; axial section (length 640 μm), with a few pillars developed in last two whorls only, × 155. Fig. 10, BMNH P 52588, from Jebel Madar, Oman, sample MS 91, Shuaiba Formation, early Aptian; axial section (length 2010 μm), with pillars only in the last-formed whorl, × 60. Fig. 11, BMNH P 52589, from United Arab Emirates, well Zakum-1, Shuaiba Formation, Aptian; axial section (length 2720 μm), with intermittently developed partial pillars in last whorls, × 40. Fig. 12, BMNH P 52590, Oman, sample WM 99 (1-240a), Wadi Mi'aidin, Natih Formation, Middle Cenomanian; axial section (length 3280 μm); same specimen as that figured by Simmons & Hart (1987: fig. 10.9.i), with the early half of the test being like *P. infracretacea* and the latter half being like *Chrysalidina*, with abundant pillars, × 35.

Fig. 13 Morphologically intermediate form between *Praechrysalidina infracretacea* Luperto Sinni and *Dukhania conica* Henson; BMNH P 52591, from northern Iraq, Mosul region, well Mushorah-1, 7435–7440 ft depth, Qamchuqa Formation, Albian; axial section (length 520 μm), with a few, incomplete pillars, in the last whorl only, × 145.
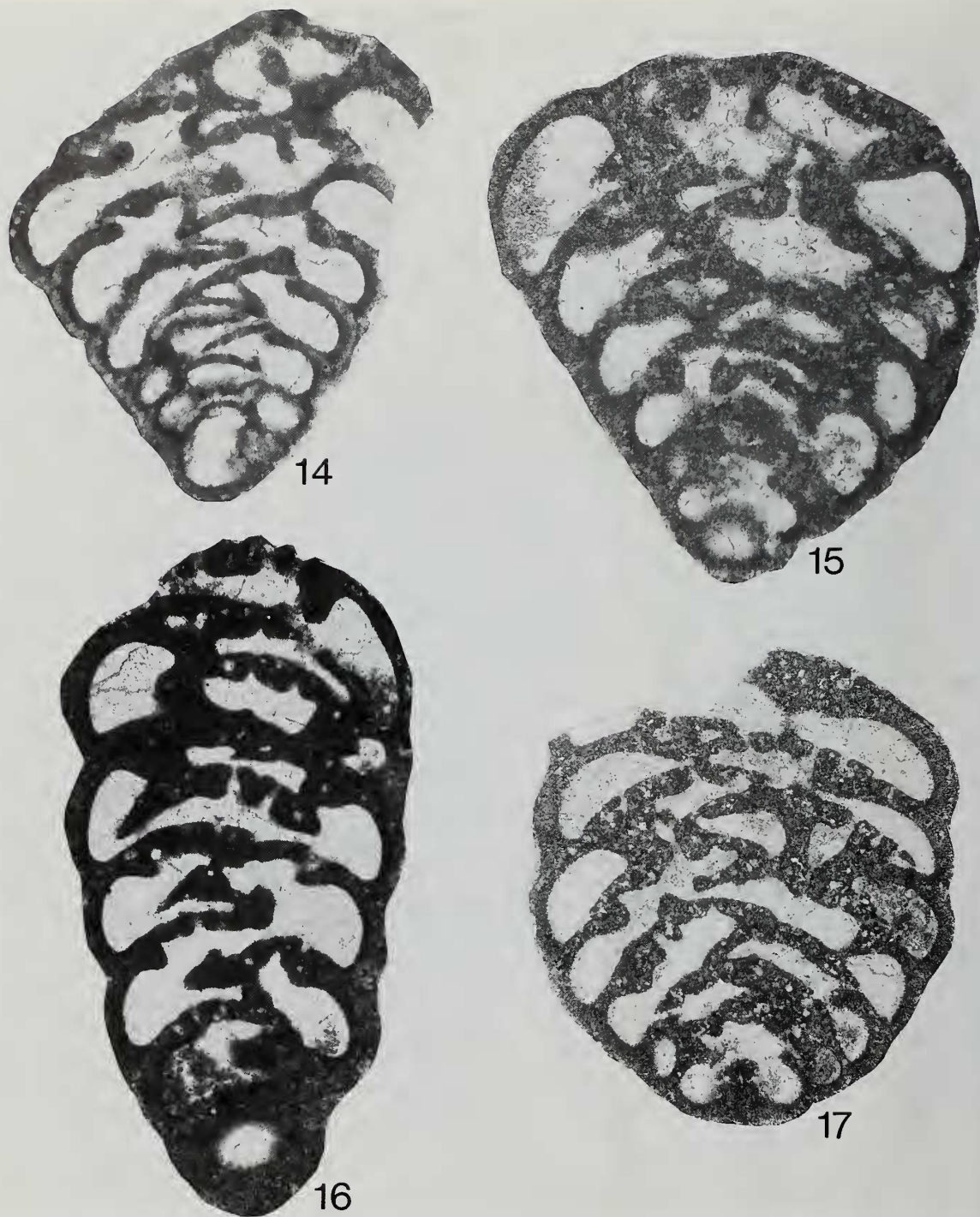
Figs 14–15 Specimens morphologically intermediate between *Praechrysalidina infracretacea* Luperto Sinni and *Dukhania conica* Henson. Fig. 14, BMNH P 52592, from northern Iraq, Mosul region, well Mushorah-1, 7470–7475 ft depth, Qamchuqa Formation, Albian; axial section (length 630 μm), with incomplete, and rare complete, pillars in last two whorls only; × 125. Fig. 15, BMNH P 52593, from Deh Luran, Iran, Cenomanian; axial section, with pillars developed throughout the umbilical areas of the last three whorls (and incomplete pillars in a previous whorl); this is a true *Dukhania*, but the chambers still retain the ancestral form (and the specimen was labelled 'Aff. *Dukhania conica* Henson' by Henson and his associates); axial section (length 1500 μm), × 55.

Fig. 16 Specimen morphologically intermediate between *Praechrysalidina infracretacea* Luperto Sinni and *Chrysalidina gradata* d'Orbigny; BMNH P 52594, from Tong-i-Mawari, Qashqai-Sarhad, Iran, 'Middle Cretaceous'; axial section (length 2620 μm), with a few pillars in the umbilical region of the last whorls, × 40.

Fig. 17 *Dukhania conica* Henson, paratype, BMNH P 52595, from 'Middle Cretaceous' (almost certainly Cenomanian), Kuh-i-Bingistan, Iran; axial section (length 960 μm), × 80.
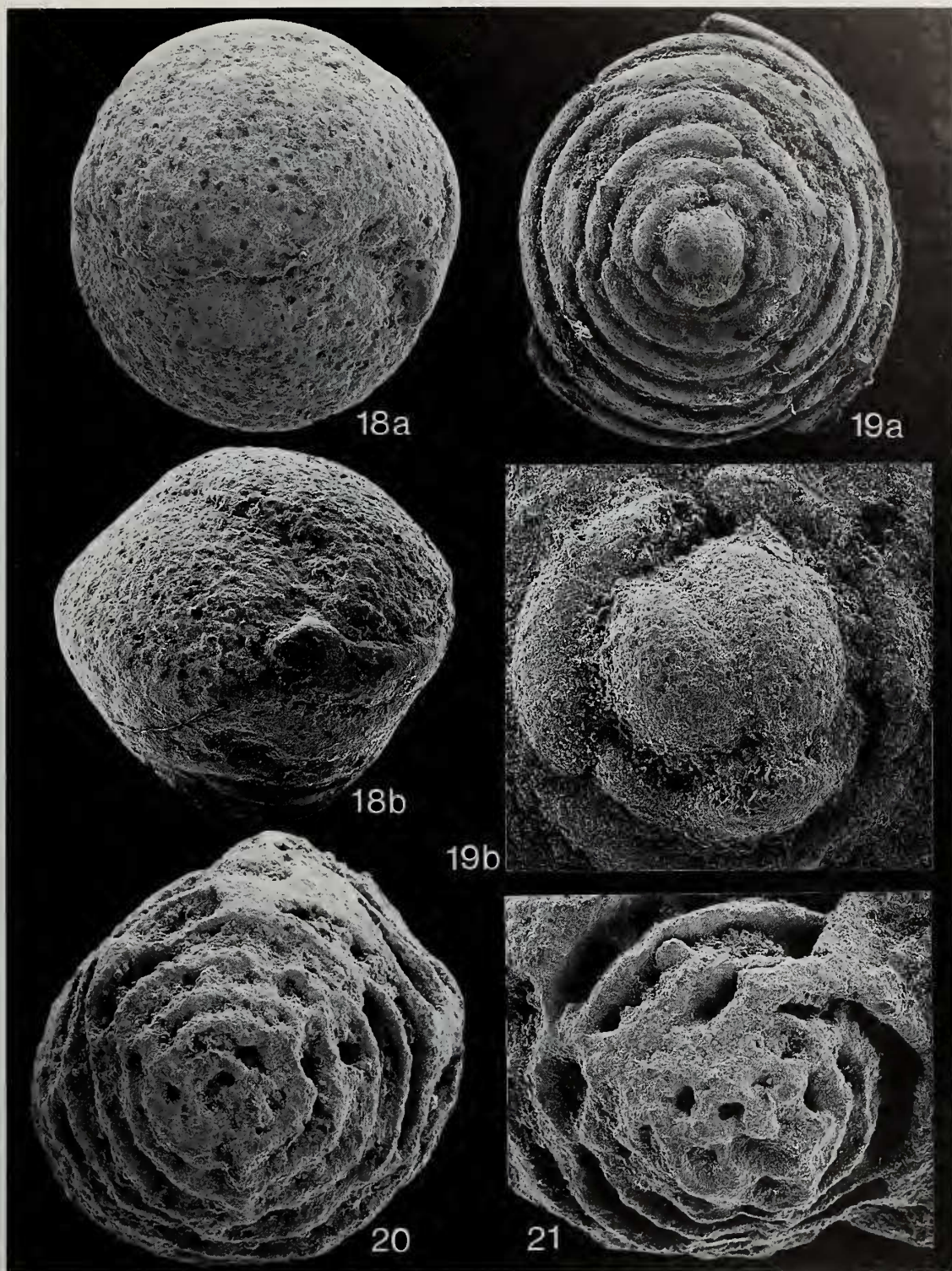
Figs **18–21** *Dukhania conica* Henson. Figs 18a–b, BMNH P 52596, from Qatar, well Dukhan-3, 2560–2565 ft depth, Cenomanian ('Middle Cretaceous'), originally determined by V. J. John but accepted by F. R. S. Henson, and believed by us to be virtually identical to the holotype of the species (BMNH P 39102); a, terminal view (showing terminal biseriality, and cribrate apertural pores calcite infilled), diameter 1880 μm, × 40; b, axial view, × 40. Figs 19a–b, paratype, BMNH P 52597, from Qatar, well Dukhan-3, 2030–2060 ft depth, Cenomanian; megalospheric form viewed from initial end, diameter 1620 μm; a, × 50; b, enlargement of nepiont, × 150. Figs 20–21, paratypes, from Qatar, well Dukhan-3, 2030–2060 ft depth, Cenomanian; microspheric forms, viewed from initial end. Fig. 20, BMNH P 52598, diameter of test 1640 μm, × 50. Fig. 21, BMNH P 52599, × 70.
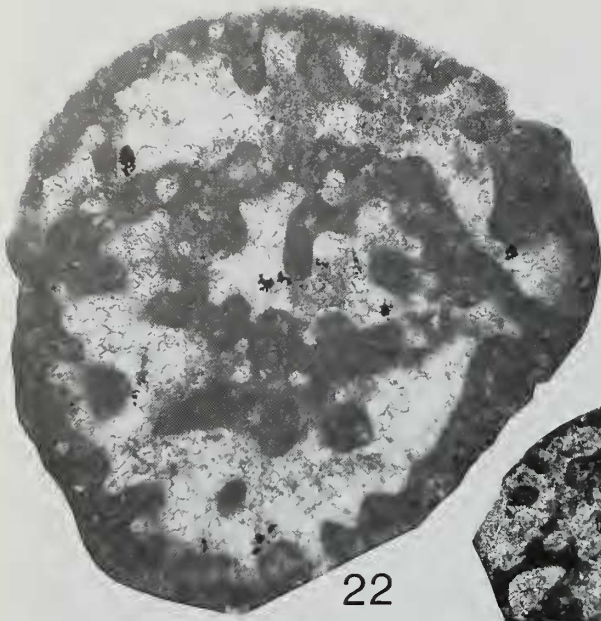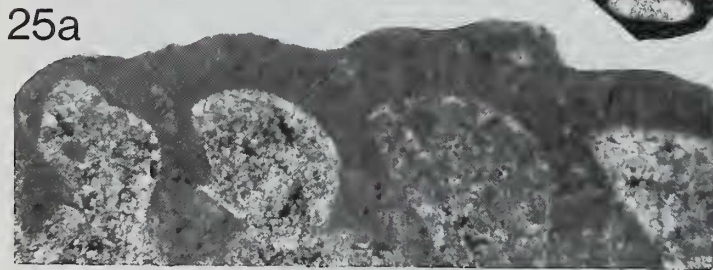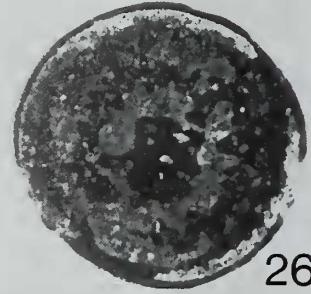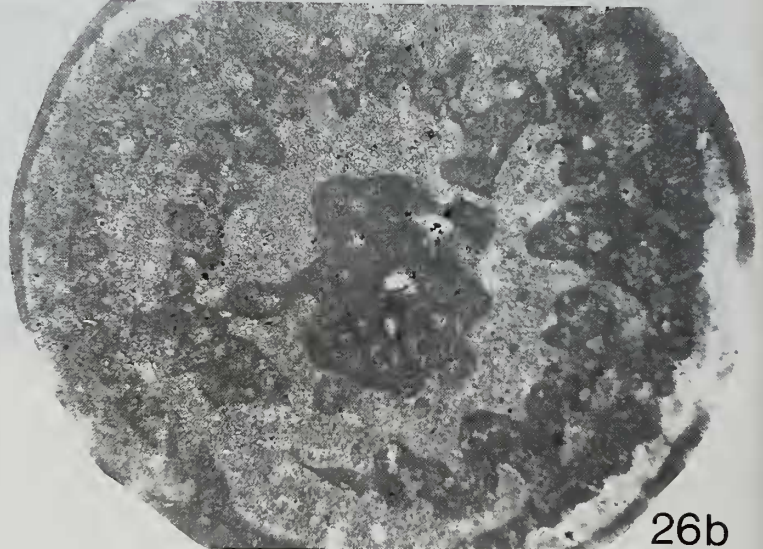
frequently than in *Praechrysalidina*; that genus may only become protocanaliculate.

PROVENANCE OF TYPES. The holotype and paratypes of *Dukhania conica* Henson were obtained from well cuttings at 2540–2570 ft depth, well Dukhan-3, Qatar, from beds called 'Middle Cretaceous' by Henson (1948) but which also contained *Praealveolina cretacea* (d'Archiac) and which are therefore probably referable to the mid or late Cenomanian (see Schroeder & Neumann, 1985).

DISTRIBUTION. Of the other occurrences recorded by Henson (1948: 616), those from the Cenomanian limestone of the Bekhme Gorge, Iraq, have few or no pillars, are morphologically transitional from *Praechrysalidina*, and are closely similar to the specimen figured (as '*Chrysalidina* cf. *gradata* d'Orbigny') from Upper Cenomanian limestone of Lebanon by Hamaoui & Saint-Marc (1970: pl. 39, fig. 2).

Specimens which are clearly intermediate morphologically between *Praechrysalidina infracretacea* and *Dukhania conica* occur in the Albian Qamchuqa Formation of the Mosul region, Iraq, where incomplete pillars, which fail to span the distance between successive apertural flaps, occur (Fig. 13) and sometimes may be accompanied by a few, complete pillars developed only in the last one or two whorls (Fig. 14). The evolution from *Praechrysalidina* to *Dukhania* seems to have been gradual and continuous during the Albian and Cenomanian, with true *D. conica* first appearing in the Cenomanian (Fig. 106, p. 150).

Specimens (Fig. 15) from the Cenomanian of Deh Luran, Iran, which occur in micritic limestones with both *Praealveolina* and *Chrysalidina gradata*, which were listed by Henson (1948: 616) as ideotypes of *Dukhania conica*, but which were labelled 'Aff. *Dukhania conica*' by Henson and his associates, have inter-flap complete pillars developed in the last three whorls and are true *Dukhania*, but the shape and proportions of their chambers still recall their ancestry.

True *Dukhania conica* is known from Qatar (Figs 18–26), Iran (Fig. 17), Iraq (Dunnington *et al.* 1959: 230), and Oman (Smith *et al.* 1990: 37, fig. 6d). The last of these (from the Middle Cenomanian part of the Natih Formation of Oman) has even more numerous pillars than the typical *Dukhania conica*, but it lacks the heavy, thick pillars, thicker chamber walls, higher chambers and larger, more elongate test characteristic of *Chrysalidina gradata* (Figs 27–30 herein and, e.g., de Castro, 1981: pls 5, 6). With such random thin sections, it is often not possible to determine directly whether the test is terminally biserial (*Dukhania*) or triserial (*Chrysalidina*).

Dukhania conica is not yet known with certainty beyond the Middle East, and, consequently, it is believed to have been palaeobiogeographically more limited than either its ancestral *Praechrysalidina* or its contemporary *Chrysalidina*. It is probable that the evolution of *Dukhania* occurred in central Tethys and that (unlike *Chrysalidina*) it did not spread, eastwards or westwards, from this area.

STRATIGRAPHY. The evolution of *Dukhania* from *Praechrysalidina* (Fig. 106) may have begun in the Late Aptian; the descendant forms, in the Albian (e.g., Figs 13–16), with partly formed inter-flap pillars and low main chambers, probably should be distinguished from the pillarless ancestor by being named *Dukhania* sp. The genus may therefore be considered to range upwards from the Albian (or even late Aptian), but *D. conica* itself is not known in beds older than Cenomanian, and it is not known to have existed later than that stage. The record by Henson (1948: 616) of *D. conica* in 'Turonian limestones', at 'Rekhme, Palestine', has not yet been substantiated.

Genus *CHRYSALIDINA* d'Orbigny, 1839

TYPE SPECIES. *Chrysalidina gradata* d'Orbigny, 1839.

Chrysalidina gradata d'Orbigny, 1839   Figs 27–34

1839   *Chrysalidina gradata* d'Orbigny: 109.
1846   *Chrysalidina gradata* d'Orbigny: 194–195; pl. 21, figs 32, 33.

REMARKS. *Chrysalidina gradata* was first described by d'Orbigny (1839, 1846) from the Cenomanian of Île Madame (Charente-Maritime, off the west coast of France) and solid specimens of topotypes, and their orientated thin sections, have been well described and photomicrographed by Azzaroli & Reichel (1965), Neumann (1967: pl. 44), de Castro (1981, and in Schroeder & Neumann, 1985) and Loeblich & Tappan (1988: pl. 204). Other specimens, in thin section, have been photomicrographed from the mid to late Cenomanian of Aquitaine, south France (Neumann 1967, *loc.cit.*), Italy (Azzaroli & Reichel 1965, de Castro 1981: pl. 7), Greece (Septfontaine 1981), Oman (Simmons & Hart 1987: pl. 10.1; Smith *et al.* 1990), Yemen (Sartorio & Venturini 1988: 116), etc. The genus is monotypic, and probably is confined to the mid Cenomanian and the earlier part of the late Cenomanian; Turonian records (Loeblich & Tappan 1988: 186) have yet to be confirmed.

As noted above, the species evolved smoothly from *Praechrysalidina infracretacea* (Fig. 106) by developing higher chambers, heavy inter-flap pillars in the umbilicus, and a longer (and larger) adult test which nevertheless retained triseriality to the end of its life. The evolution seems to have been slow and completely gradational; although it began in the late Aptian (Figs 10–11) and continued through the Albian (Fig. 9), with the beginnings of the development of pillars in slender, triserial tests (which were, otherwise, typical *Praechrysalidina*), true *Chrysalidina* did not appear until the Cenomanian. Even then, specimens occur which lack pillars in the neanic umbilicus, at a stage of growth when the test could remain as slender as that of the ancestral (and by now extinct) *P. infracretacea* (Fig. 12). The typical


Figs 22–26   *Dukhania conica* Henson, from Qatar, well Dukhan-3, Cenomanian. Fig. 22, paratype, BMNH P 39105, from 2550–2560 ft depth; equatorial section (diameter 1500 μm), × 60. Fig. 23, topotype, BMNH P 52600, from 2560–2565 ft depth; axial section (length 2160 μm), × 35. Fig. 24, paratype, BMNH P 39104, from 2540–2570 ft depth; axial section (length 2080 μm), × 30. Figs 25a–b, paratype, BMNH P 52601, from 2540–2570 ft depth; a, wall with canaliculi, × 890; b, whole axial section (length 2060 μm), × 35. Figs 26a–b, paratype, BMNH P 52602, from 2030–2060 ft depth; a, equatorial section (breadth 1840 μm), showing ultimate biseriality, × 20; b, enlargement, showing umbilical pillars, × 515.
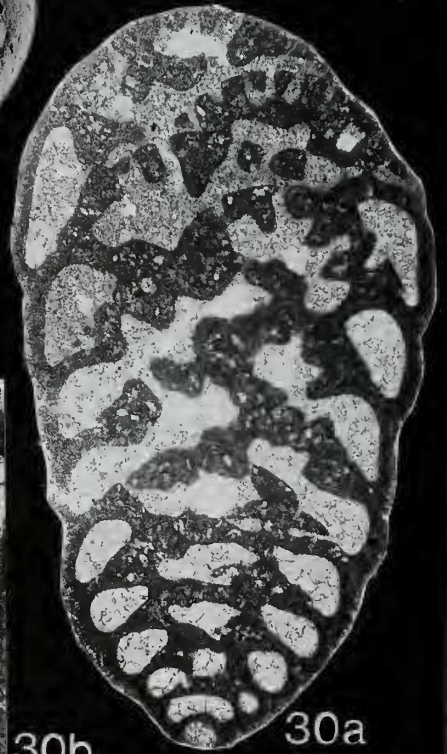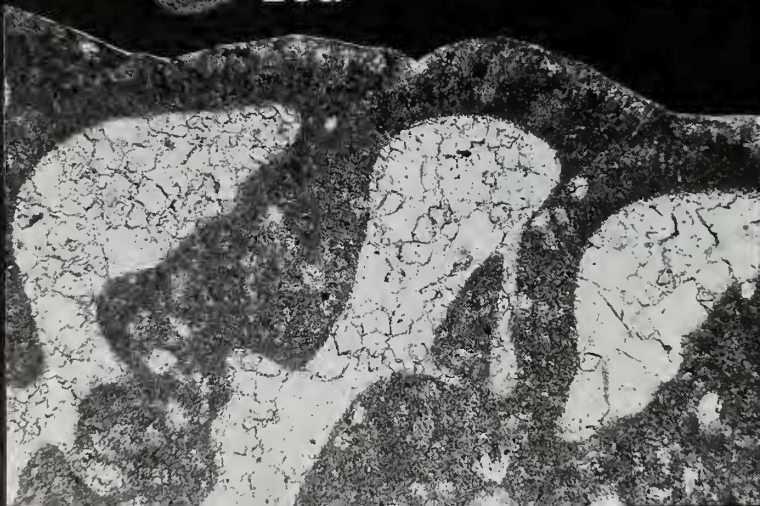
27a

27b

28

29a

29b

30b

30a
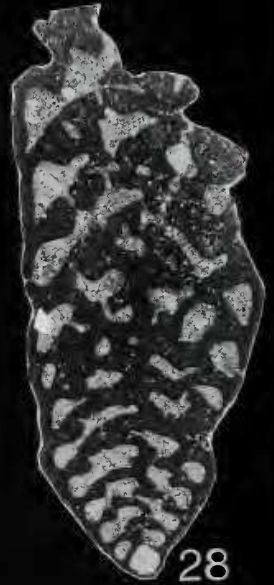
C. gradata (Figs 27–30) rapidly tapered initially, in its neanic growth stage, although its ephebic chambers enlarged much more slowly; heavy umbilical pillars characteristically developed in all post-nepionic whorls.

The walls of many specimens of *Chrysalidina gradata* remain solid throughout growth (e.g., the topotypes illustrated here, Figs 27–29, and those photomicrographed by de Castro, 1981: pls 5, 6); this is not an appearance resulting from diagenetic alteration, because the presence and orientation of intramural quartz grains would have prevented the primary development of protocanaliculation and canaliculi. However, other topotypes show the development of protocanaliculation or canaliculi even in the ontogenetically early walls (Figs 30a–b herein, and, e.g., Loeblich & Tappan, 1988: pl. 204, fig. 5). The canaliculi of some late Cenomanian, Italian specimens are so clear that de Castro (1981: pl. 7) called them '*Chrysalidina* cf. *gradata*'. However, we can see no way to separate taxonomically the solid walled forms, the protocanaliculate forms and those with canaliculi; they are otherwise structurally identical, are indistinguishable without thin-sectioning or the SEM examination of partly-eroded specimens, occur in the same assemblages and appear to have the same stratigraphic range within the mid to late Cenomanian.

Accordiella conica Farinacci is a monotypic genus which was first recorded from the Lower Senonian of Italy (Farinacci 1962), when it was noted that it was also known from the Coniacian–Santonian of France (Aquitaine) and Spain. It has not yet been observed in the Middle East or recorded from the Turonian (for example, it was not recorded from the Albian–Turonian interval of the Mediterranean region by Schroeder & Neumann, 1985). Nevertheless, the evolution of *Accordiella* from *Chrysalidina* (as postulated by Septfontaine, 1981: 184 – Farinacci, 1962: 10, suggested an evolution directly from *Dukhania*) is very likely to be correct: all that is required morphologically is to widen the umbilicus further, fill it with more closely spaced, more abundant pillars, and to increase the number of chambers, around the broader umbilicus, to four (i.e., to achieve quadriseriality, at least in the adult) (Farinacci 1962: pl. 1, figs 1–7). Morphologically intermediate forms may be expected in the Turonian.

The lineage is unknown in the Campanian and younger strata and probably became extinct at this time. As noted above, it is probable that the Chrysalidininae should exclude other, Cenozoic taxa (such as *Vacuovalvulina* and *Pseudochrysalidina*), but this needs further study.

Subfamily PARAVALVULININAE nov.

DIAGNOSIS. Test quadriserial or quinqueserial initially, becoming quadriserial in neanic growth, and then quinqueserial or quadriserial or triserial in the adult.

KEY TO GENERA INCLUDED

1. Umbilicus or pseudoumbilicus concave, with apertural flaps or lips attached to the lower part of the exposed apertural faces of the chambers; no internal, umbilical pillars:
   1.1. Primary and accessory apertures interiomarginal; no accessory areal, cribrate apertures; apertural flaps of successive whorls are well separated:
      1.1.1. Test quadriserial in adult: septa flattened or very weakly convex; narrow, hollow umbilicus: *Redmondoides* gen. nov. (Bajocian–Oxfordian–?Kimmeridgian).
      1.1.2. Test initially quadriserial, becoming triserial in adult; no true umbilicus:
         1.1.2.1. Septa and terminal faces flat or concave: *Riyadhoides* gen. nov. (late Bajocian–Tithonian).
         1.1.2.2. Septa and terminal faces highly convex: *Riyadhella* Redmond, 1965 (Bajocian–Kimmeridgian).
   1.2. With accessory, areal, cribrate apertures; umbilical-apertural flaps of successive whorls are broad and are axially separated by only narrow spaces (they may be appressed axially); adult test quadriserial or quinqueserial: *Pseudomarssonella* Redmond, 1965 (Bathonian–Callovian).
2. Umbilicus covered by convex umbilical flaps which are attached to the top of the apertural faes of the chambers; with accessory, areal, cribrate apertures; internal pillars between successive umbilical flaps; early test quadriserial, adult becoming triserial: *Paravalvulina* Septfontaine, 1988 (Bathonian–Valanginian–?Hauterivian).

Genus *REDMONDOIDES* nov.

TYPE SPECIES. *Pseudomarssonella media* Redmond, 1965.

DIAGNOSIS. A chrysalidinid with a test which is quinqueserial or quadriserial initially, becoming quadriserial in the adult; adult primary aperture interiomarginal, umbilical, with an apertural flap or lip (which is not penetrated by areal accessory apertures) projecting from the lowest part of the apertural face above the aperture; no internal, umbilical pillars; terminal faces and septa are flattened or only weakly convex, and make distinct angles with the uninflated chamber walls.

NAME. In further recognition of C. D. Redmond's work on Arabian Mesozoic foraminifera; gender – masculine.

DIFFERENTIATION AND AFFINITY. *Redmondoides* differs from *Pseudomarssonella* Redmond in that the latter has broad umbilical flaps, penetrated by areal, cribrate, pore-like accessory apertures; these flaps span much or all of the umbilicus and fuse to the opposite chambers (or their flaps) of the same whorl, partly or wholly closing the accessory interiomarginal aperture. In *Redmondoides* the umbilical flaps (or 'lips') are much narrower and the interiomarginal aperture remains unimpeded. *Riyadhoides* has no umbilicus or umbilical flaps, and also differs in its quadriserial–triserial coiling (a coiling mode which can result in a distinctly parallel-sided adult test, but which can also produce a conical, rapidly tapering one).

---

gs **27–30** *Chrysalidina gradata* d'Orbigny, topotypes, from Île Madame, Charente Inférieur, France, Cenomanian; Figs 27a–b, BMNH P 52603, terminal and axial views (length 1940 µm), × 40. Fig. 28, BMNH P 52604, axial section (length 3860 µm), × 20. Figs 29a–b, BMNH P 52605, axial and terminal views (length 2120 µm), × 40. Figs 30a–b, BMNH P 53606, axial section (length 3260 µm); a, × 30; b, detail showing solid septa with randomly arranged calcareous microgranules and included silt grains, and protocanaliculate–canaliculate chamber walls, × 105.
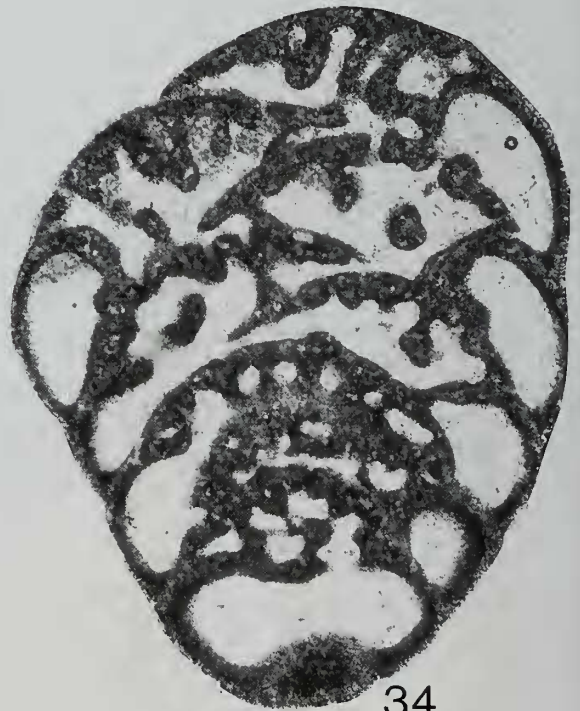
Figs 31–34 *Chrysalidina gradata* d'Orbigny. Axial sections. Figs 31–32, 34, from Oman, Jebel Madamar, Natih Formation, Cenomanian. Fig. 31, BMNH P 52607, sample WMA 1 (length 2020 μm), × 45. Fig. 32, BMNH P 52609, sample WMA 3, same specimen as that figured by Smith, Simmons & Racey, 1990, fig. 6d (length 2450 μ), × 35. Fig. 33, from Deh Luran, Iran, Cenomanian, BMNH P 39127, from the same limestone thin section as the specimen figured by Henson, 1948: pl. 15, fig. 8 (length 2700 μm), × 40. Fig. 34, BMNH P 52608, sample WMA 1 (length 2400 μm), × 40.
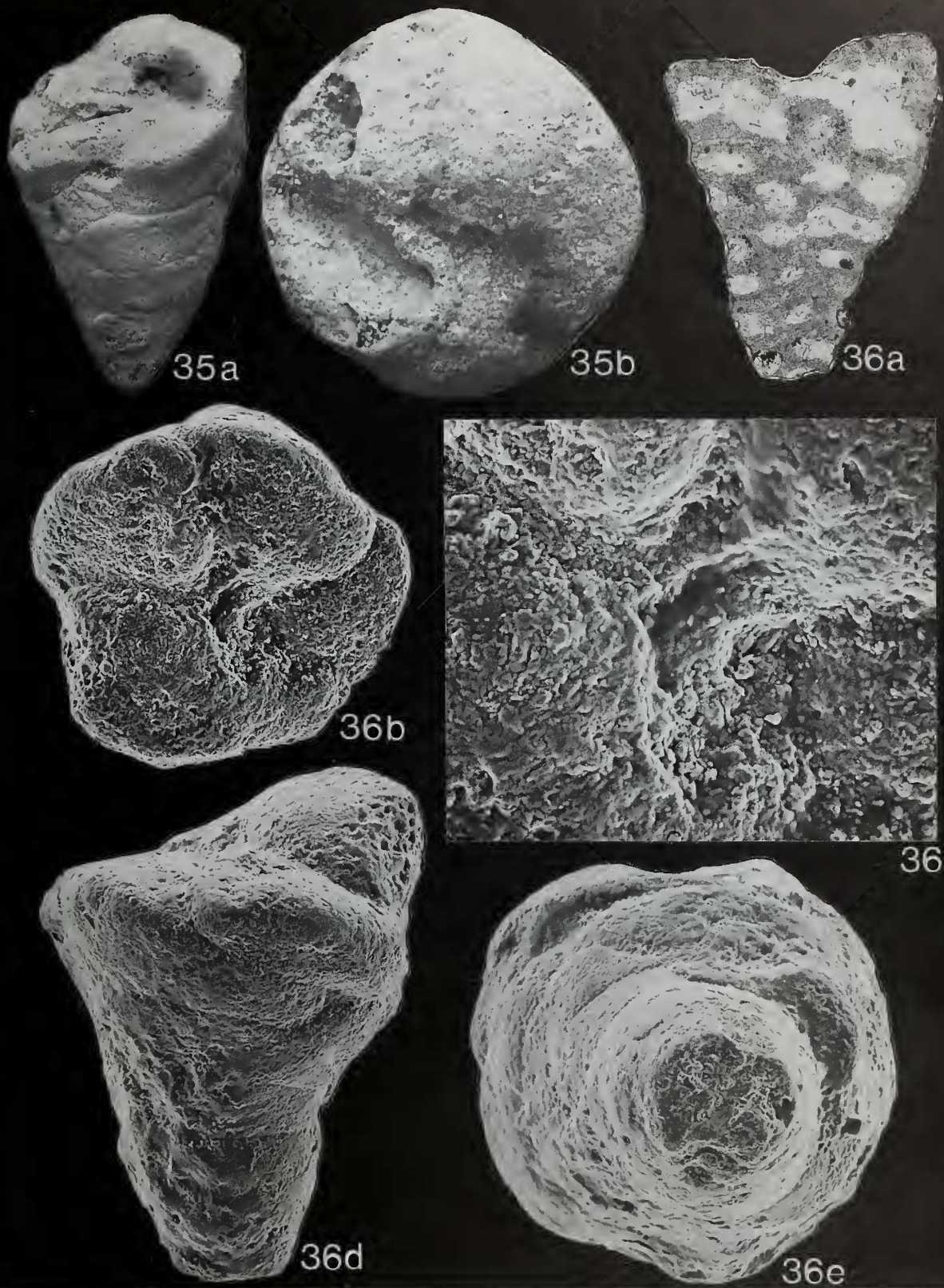
Figs 35–36 *Redmondoides medius* (Redmond), from Saudi Arabia, Aramco well 4A, 4148 ft depth, Upper Dhruma Formation, Middle Callovian. Figs 35a–b, holotype AMNH FT-1267; a, axial view (length 450 µm), × 145; b, terminal view, × 220. Figs 36a–e, paratype AMNH FT-1268; a, axial section (formed after preparation of Figs 36b–e), length 400 µm, × 150; b, terminal view, × 200; c, enlargement of umbilical area, × 500; d, axial view (showing open canaliculi in wall of last chamber), in same attitude as the thin section (Fig. 36a), × 220; e, initial view, showing initial quadriseriality, × 220.

Riyadhella differs in its highly convex terminal faces and septa, which do not form distinct angles with the lateral chamber walls; it also lacks an umbilicus and an apertural flap, and has terminal triseriality.

It is supposed that *Redmondoides* gave rise to *Pseudomarssonella* in the Bathonian, which, in turn, gave rise to *Paravalvulina* Septfontaine, also in the Bathonian.

SPECIES INCLUDED AND STRATIGRAPHY. In addition to the type species, the following are now included in *Redmondoides*: *Pseudomarssonella biangulata* Redmond (synonym of *R. medius*), *P. inflata* Redmond, *P. primitiva* Redmond, *Riyadhella rotundata* Redmond, *Valvulina lugeoni* Septfontaine. The known stratigraphic range of the genus is Bajocian–Oxfordian–?Kimmeridgian. It is known (principally by specimens referable to *Redmondoides lugeoni*) in marine deposits from western to eastern Tethys (from southern Europe to Borneo). Random thin sections of specimens, which may be species of *Redmondoides,* are known to us from very early Cretaceous (possibly Valanginian–Hauterivian), Tethyan limestones, but the seriality of their chamber arrangement is unknown and their generic identity cannot yet be established.

In the following descriptions, the species originally described by Redmond are described first, and these are followed by an emended description of *Redmondoides lugeoni* (Septfontaine).

Redmondoides medius (Redmond, 1965)   Figs 35–37

1965   *Pseudomarssonella media* Redmond: 135; pl. 1, figs 11–13.
1965   *Pseudomarssonella biangulata* Redmond: 134; pl. 1, fig. 1.
1989   *Pseudomarssonella bipartita* Redmond; Delance & Ruget: 206; pl. 3, fig. 16 (*non* Redmond, 1965).

DESCRIPTION EMENDED. Test walls and septa of microgranular calcite, with little or no adventitious agglutinated material present; the walls are initially solid, but may become canaliculate in the last-formed chambers. The test may be quinqueserial in the nepionic growth stage but is quadriserial in the neanic and ephebic stages. The test is subcircular in equatorial section. The neanic growth stage may taper slowly, at about 30°–40°, but ephebic growth enlarges the chambers more rapidly, so that the adult test is a cone tapering at about 50° (in some specimens, the 50° taper occurs in all growth stages).

The chambers are about three times as broad as high, and constitute the outer 40% or more of the test diameter; the central 15%–20% of the equatorial diameter is umbilical. The terminal face of each chamber is about as thick as the lateral wall, but the intercameral septa are virtually doubled in thickness by being composed of two layers – the terminal wall of the earlier chamber plus the basal wall of the succeeding chamber. The double-thickness septum is about one-third as high as the chambers (i.e., the lumina of a chamber is about twice as high as the septum which precedes it). The terminal faces and the septa are flattened, and make angles of 70°–90° with the lateral walls. The lateral walls are flattened or slightly concave. The intercameral sutures are very shallowly and narrowly depressed or are not depressed at all.

The apertural face is very low. The interiomarginal, umbilical aperture is furnished with a thin, narrow, apertural lip. The umbilicus is depressed and empty.

REMARKS. Redmond (1965) distinguished *Pseudomarssonella biangulata* from *P. media* by the supposed 'break between growth stages' in the former, whereas the latter had 'sides diverging at a uniform rate'. However, a paratype of *P. media* (Fig. 36) has the same slender neanic stage and more widely conic ephebic stage as the holotype of *P. biangulata* (Fig. 37).

The present authors can find no way of satisfactorily distinguishing between the two taxa, and, as first revisers (ICZN Article 24), choose *P. media* to be the senior synonym. Redmond (1965) stated that *P. biangulata* was 'common in the upper part of the middle Dhruma Formation', but only the holotype of this species (no paratypes or other specimens) was deposited; in comparison, the holotype and two paratypes (one now sectioned) of *P. media* ('abundant . . . [in] the upper Dhruma Formation') were deposited.

The specimen figured by Delance & Ruget (1989) as '*Pseudomarssonella bipartita*' is poorly preserved and its identity is uncertain; however, it appears to have terminal quadriseriality and a small, flattened umbilical area, which, together with its overall test shape, indicates that it should be referred to *Redmondoides medius*.

DIFFERENTIATION. *Redmondoides medius* is less slender and less slowly tapering than *R. primitivus*, and more slender and more slowly tapering than *R. inflatus*. Otherwise, these three 'species' are very similar. Redmond and his co-workers in Aramco succeeded in distinguishing them; further work is needed before one can be certain that the distinctions can be maintained.

Redmondoides rotundatus (Redmond) is distinguishable by its more broadly depressed intercameral sutures and more convex terminal faces. *R. lugeoni* (Septfontaine) also differs by its broader umbilicus and much broader apertural lip.

PROVENANCE OF TYPES. The type specimens of *R. medius* were obtained from Aramco stratigraphic well 4A (27°51′19″N, 44°54′47″E), from a core at 4148 ft depth, and that of *R. biangulatus* came from Aramco drill hole T 60 A (24°55′04″N, 45°59′08″E), from 80–90 ft depth.

STRATIGRAPHY. Redmond (1965) recorded '*Pseudomarssonella*' *biangulata* from the upper part of the middle Dhruma Formation ('Bathonian') and '*P.*' *media* from the upper part of the upper Dhruma Formation ('Callovian'); these intervals were referred by Powers (1968) to the *Dhrumaites* Zone limestone and shale ('Unit 8', uppermost Middle Dhruma) and the Hisyan (or Hishyan) Member (shales, 'Unit 10', upper Upper Dhruma), repectively. The former was regarded by Enay *et al.* (1987) as belonging to the Middle (or Late) Bathonian, and the latter as being referable to the Middle Callovian.

The specimens described by Delance & Ruget (1989) were obtained from the Bathonian of the Nivernais, France, east of the Loire, at about 47°10′N, 3°15′E.

Redmondoides inflatus (Redmond, 1965)   Figs 38–39

1890   *Valvulina conica* Parker & Jones; Haeusler: 76; pl. 12, figs 27–35 (*non Valvulina triangularis* d'Orbigny var. *conica* Parker & Jones, 1865)
1965   *Pseudomarssonella inflata* Redmond: 134–135; pl. 1, figs 4–5.

DIFFERENTIATION. This taxon seems to be identical to *R. medius* (Redmond) except for the broader, more rapidly tapering test, in which the subconical test tapers at angles o
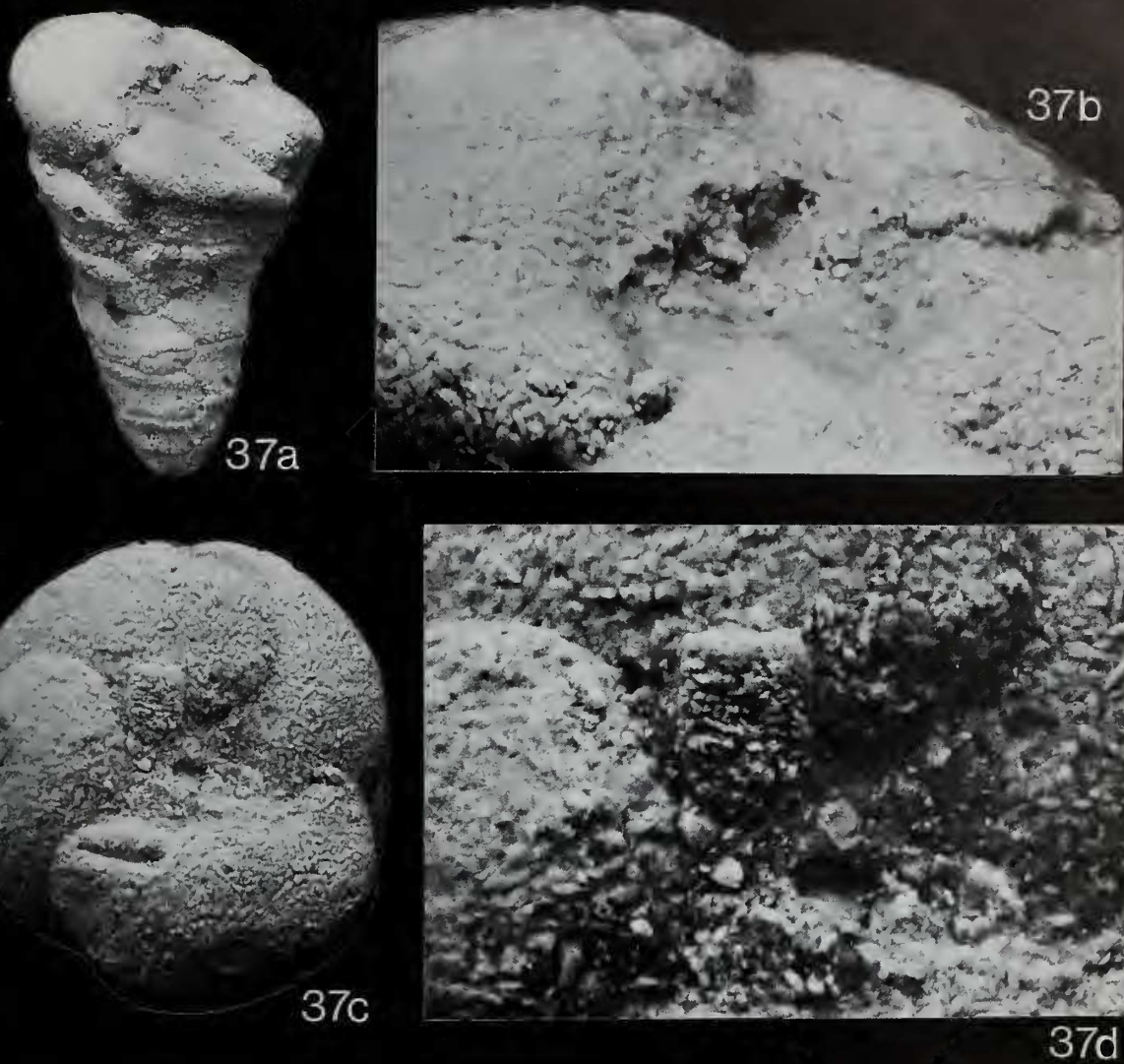
Fig. 37 *Redmondoides medius* (Redmond). Holotype of the synonymous *Pseudomarssonella biangulata* Redmond, AMNH FT-1264; from Saudi Arabia, Aramco T 60 A, 80–90 ft depth, Middle Dhruma Formation, mid or late Bathonian; a, axial view (length 380 μm), × 170; b, enlargement of apertural area, × 590; c, terminal view, × 270; d, enlargement of umbilical area, × 640, showing 'spicule-like' coating of the surface.

60° (paratype) to 80° (holotype), and the broader umbilicus (about 25% of the total test breadth).

REMARKS. Only the holotype and one paratype were deposited. There is insufficient information to confirm that this represents a species distinct from *R. medius*. However, the type specimens appear to be identical with those illustrated by Haeusler (1890) from the 'Transversariusschichten' (the '*Ammonites transversarius* Zone') of the Lower Oxfordian of Switzerland (Haeusler misidentified his specimens as the Cenozoic true *Valvulina*, *V. triangularis* d'Orbigny *conica* Parker & Jones, 1865); they have identical late quadriseriality, chamber and test shapes.

Redmond (1965) stated that there were 'five chambers in the final whorl'; the last chamber of the holotype is broken but could well have originally occupied about one-quarter of the final whorl, while the paratype is clearly quadriserial terminally.

PROVENANCE OF TYPES. From Aramco stratigraphic well 4A (as the type specimens of *R. medius*), core at 4524 ft depth.

STRATIGRAPHY. Recorded by Redmond (1965) from the 'upper part of the middle Dhruma Formation. Bathonian', the same as for the type of *R. biangulatus* (Redmond), the junior synonym of *R. medius* (Redmond). This interval would be that called 'Unit 8' by Powers (1968) or 'D6' by Enay *et al.*

Figs 38–39   *Redmondoides inflatus* (Redmond); from Saudi Arabia, Aramco well 4A, 4524 ft depth, upper Middle Dhruma Formation, mid or late Bathonian. Figs 38a–b, holotype, AMNH FT-1267; a, axial view (length 450 µm), × 145; b, terminal view, × 165. Figs 39a–b, paratype, AMNH FT-1268; a, axial view (length 420 µm), × 150; b, terminal view, × 165.

(1987); the latter considered it to be referable to the mid/late Bathonian.
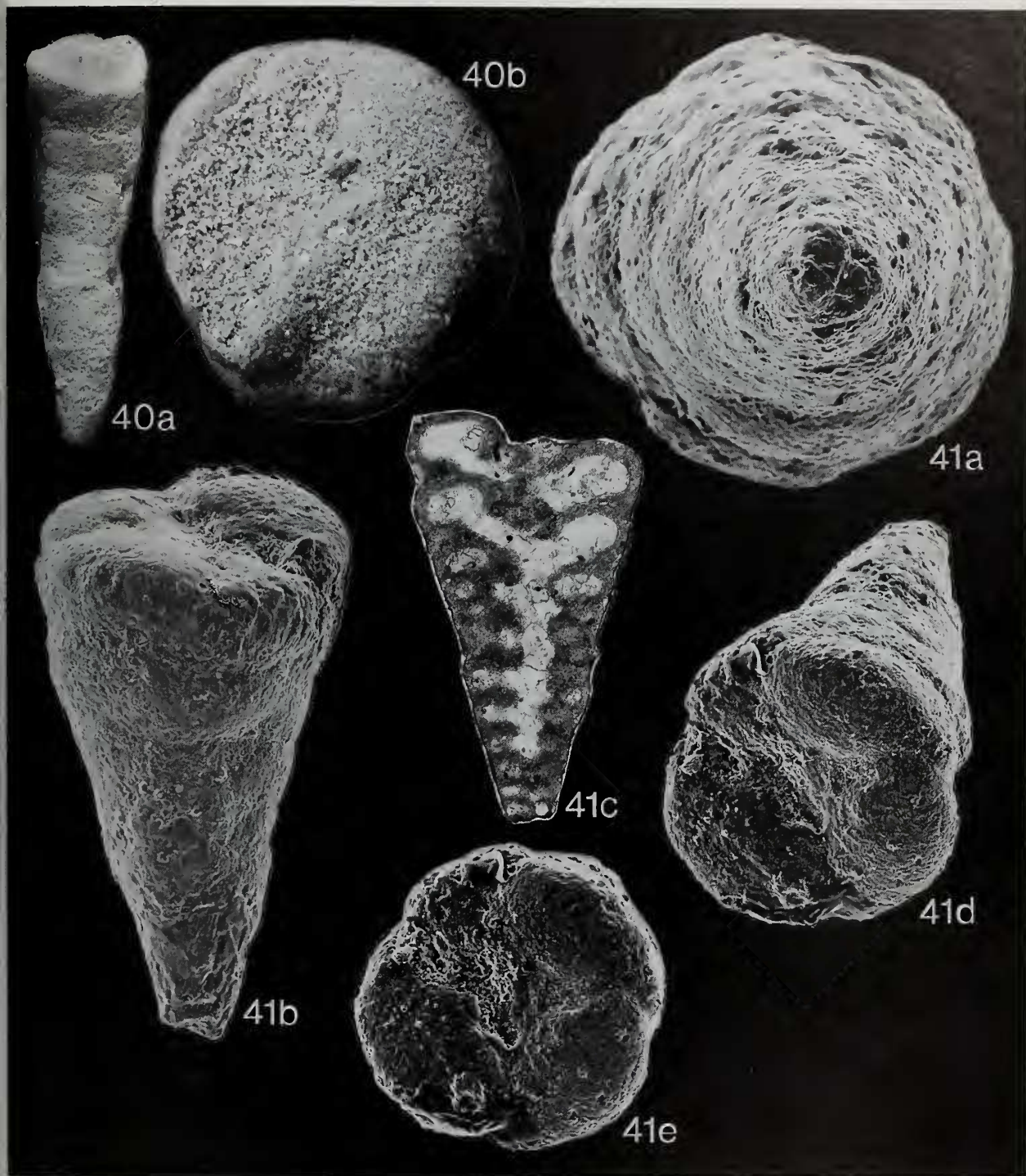
Redmondoides primitivus (Redmond, 1965)   Figs 40–41

1965   *Pseudomarssonella primitiva* Redmond: 136; pl. 1, figs 16–18.

DESCRIPTION EMENDED. Test walls and septa of microgranular calcite, with little or no adventitious agglutinated material present. The walls are thin and solid, and no canaliculation is yet known. The test may be quinqueserial nepionically, but it is quadriseral throughout the remainder of growth. It is subcircular in equatorial section, and forms a narrow, slender cone, with a 30°–35° initial angle. The test may (as in the

holotype) narrow after neanic growth, to taper terminally at only 20° or less, but it may retain a constant rate of chamber enlargement (and constant angle of taper) throughout ontogeny.

The chambers are about three times as broad as high and constitute the outer 35% of the test diameter; the central 30% of the equatorial diameter is umbilical. The terminal face of each chamber is about as thick as the lateral wall, and the intercameral septa are only partially thickened by the deposition, over their outer parts, of a thin basal layer of the succeeding chamber wall. Even the double-thickened septa may only be a quarter as high as the chambers theselves.

The terminal faces and the septa are flattened or only very weakly convex, and make angles of 90° or more with the uninflated or only slightly inflated lateral chamber

Figs 40–41 *Redmondoides primitivus* (Redmond); from Saudi Arabia, Riyadh Water Well-1, 2400–2410 ft depth, Middle Dhruma Formation, late Bajocian. Figs 40a–b, holotype AMNH FT-1277; a, axial view (length 680 μm), × 100; b, terminal view, × 290. Figs 41a–e, paratype AMNH FT-1278 (Figs 41a, b, d, e are the original, solid specimen, now sectioned as Fig. 41c); a, initial view, × 250; b, axial view (length 540 μm), × 175; c, axial section, × 130; d, oblique terminal view, × 175; e, terminal view, × 175.

42a 42b 43a 44a 44b 43b 44c 45a 45b
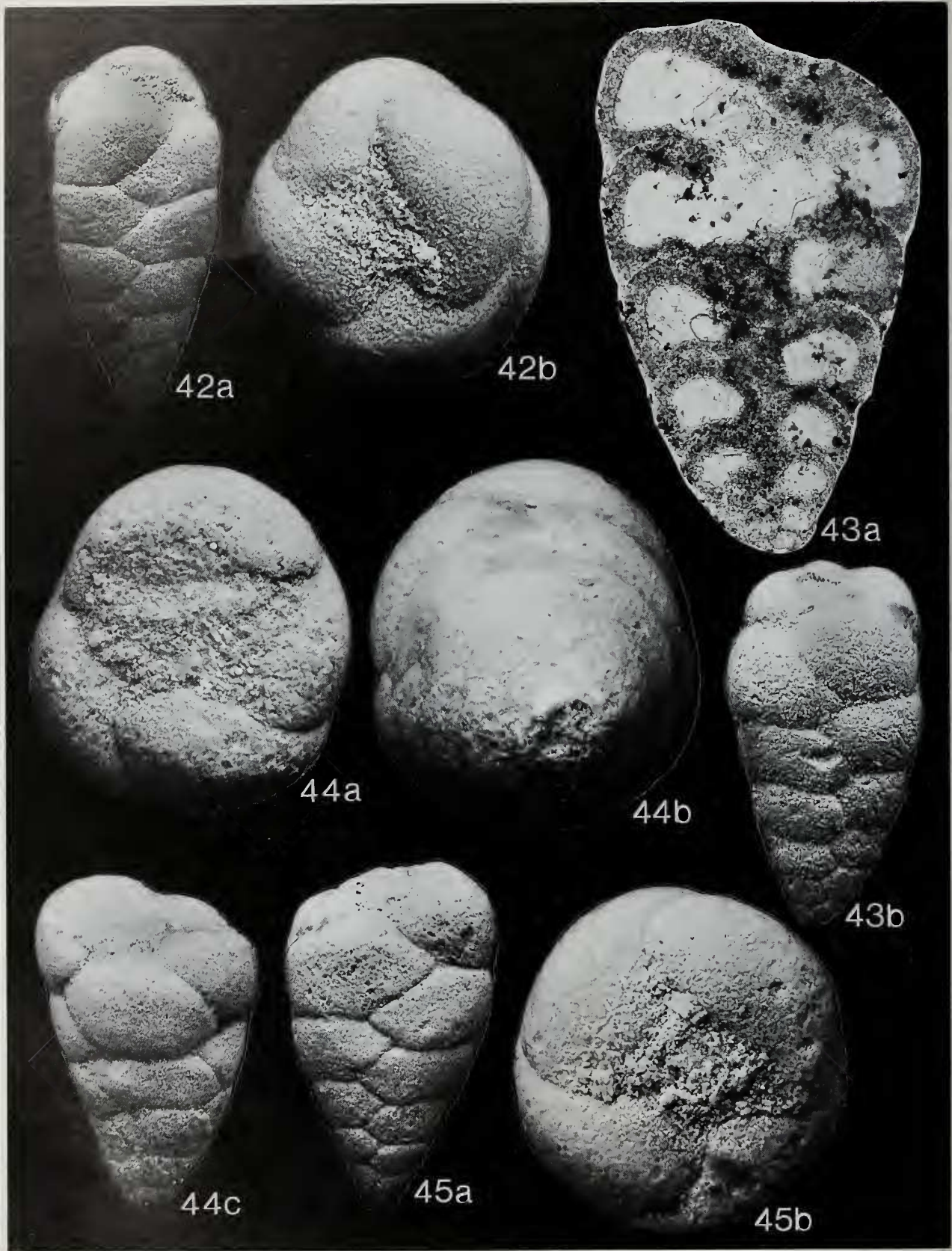
walls. Externally, the intercameral sutures are shallowly depressed.

The apertural face is low. The interiomarginal, umbilical aperture has a narrow, thin lip. The umbilicus is depressed and empty.

DIFFERENTIATION. This species differs from *Redmondoides medius* (Redmond) principally by its slender, slowly tapering test and its partially doubled septa. It is otherwise morphologically very similar to *R. medius* and to *Riyadhoides mcclurei* (Redmond), from which it differs in its terminally quadriserial (not triserial) test.

REMARKS. Redmond (1965) noted that *Redmondoides primitivus* occurred at stratigraphically older levels than *Riyadhoides mcclurei*; it is probable that *Redmondoides primitivus* was ancestral to both *Riyadhoides mcclurei*, which gained terminal triseriality, and to *Redmondoides medius*, which broadened the cone and probably gave rise to the other forms of *Redmondoides* and thence to *Pseudomarssonella* and its descendants.

PROVENANCE OF TYPES. The holotype and two paratypes were obtained by Redmond (1965) from Riyadh Water Well 1 (24°37'45"N, 46°41'06"E) at 2400–2410 ft depth, middle Dhruma Formation.

STRATIGRAPHY. This is the oldest named species of *Redmondoides*; it was reported by Redmond (1965) to occur from the uppermost part of the Lower Dhruma formation ('Upper Bajocian?') to the lower part of the Middle Dhruma ('Bathonian'). These are the intervals named by Powers (1968) 'Unit 4' (the Dhibi Limestone Member, the *Ermoceras* Zone of the uppermost Lower Dhruma) and 'Unit 5' (the *Thambites* Zone of the lowest Middle Dhruma); but they were relabelled as 'Units D2 and D3' by Enay *et al.* (1987), who referred both to the late Bajocian. We know of no reliable records of this species from beds proved to be younger than Bajocian.

Redmondoides rotundatus (Redmond, 1965)
Figs 42–45, 79

1965   *Riyadhella rotundata* Redmond: 140: pl. 1, figs 36–39.

DESCRIPTION EMENDED. Test walls and septa of microgranular calcite, with little or no adventitious agglutinated material present; the walls are initially solid, but become protocanaliculate and, ultimately, canaliculate with growth. The test is quadriserial; it is subcircular in equatorial section, with intercameral sutures weakly and very narrowly depressed, producing a smooth, not lobulate, axial profile. The test initially tapers at 55°–60°, but this reduces to 30° or less (becoming nearly parallel-sided) in the adult, as the chambers enlarge less rapidly.

The chambers are about twice as broad as high, and constitute the outer 40% of the test diameter; the central 20% of the equatorial diameter is umbilical. The terminal face of each chamber is about as thick as the (lateral) wall, but the intercameral septa, being composed of two layers (the terminal wall of a chamber plus the initial, basal wall of the next, succeeding chamber) is nearly twice as thick; even then, the double-thickness septum is less than a quarter as high as the adjacent chambers. The terminal faces of the chambers (and the preceding intercameral septa) are weakly convex, making distinct angles (initially less that 90°, terminally slightly more than 90°) with the chamber walls.

The apertural face is low and convex; the interiomarginal, umbilical aperture is furnished with a thin, narrow, apertural lip. The umbilicus is deep and empty.

REMARKS AND DIFFERENTIATION. The chambers of this species are exceptionally high (appearing nearly square in axial thin section), and it was probably for this reason that Redmond (1965) referred it to *Riyadhella*. However, the holotype and all the paratypes are terminally quadriserial, with distinct angularity between the terminal faces of the chambers and their lateral walls, clearly distinguishing it from that genus. Redmond (1965: 140) said of this species that 'most individuals have four chambers in the final whorl; only a few show a reduction to three chambers.' As stated above, none of the deposited specimens show such a reduction.

In axial thin section, the very thick intercameral septa are additional guides to identity.

STRATIGRAPHY. The holotype and paratypes were obtained from the Riyadh Water Well 1 (24°37'45"N, 46°41'06"E), 2020–2030 ft depth, from beds referred by Redmond (1965) to the Middle Dhruma Formation; he believed that the species was 'common throughout [the] upper part of the Middle Dhruma Formation, Bathonian'. In Powers (1968) the species was recorded as characteristic of the uppermost Middle Dhruma (Unit 8), the *Dhrumaites* Zone limestones and shales, 'Middle or Upper Bathonian', an interval which Enay *et al.* (1987) called 'D6' and referred to the mid/late Bathonian.

Redmondoides rotundatus is known, in random thin section, from beds as young as the Diyab Formation, Oxfordian (Fig. 79, p. 141), from subsurface sequences drilled off-shore at Qatar.

Redmondoides lugeoni (Septfontaine, 1977)
Figs 46–54, 78

1966   Valvulinids indet.; Bayliss: 176; pl. 52, figs 9–10.
1977   *Valvulina lugeoni* Septfontaine: 612–613; fig. 6; pl. 2, figs 2–5.
1977   *Valvulina lugeoni* Septfontaine; Furrer & Septfontaine: 723–724; pl. 2, figs 8–10.
1981   *Valvulina lugeoni* Septfontaine; Septfontaine: 182, 184; pl. 2, fig. 11.
1984   *Valvulina lugeoni* Septfontaine; Pélissié, Peybernès & Rey: 481–482; pl. 2, fig. 13.
1988   *Valvulina lugeoni* Septfontaine; Septfontaine: 248.

Figs 42–45   *Redmondoides rotundatus* (Redmond), from Saudi Arabia, Riyadh Water Well-1, 2020–2030 ft depth, Middle Dhruma Formation, mid or late Bathonian. Figs 42a–b, holotype AMNH FT-1292; a, axial view (length 440 μm), × 150; b, terminal view, × 230. Figs 43a–b, paratype, now sectioned, AMNH FT-1293A; a, axial section (length 450 μm), × 215; b, original axial view (original length 450 μm), × 150. Figs 44a–c, paratype AMNH FT-1293B; a, terminal view, × 200; b, initial view, × 200; c, axial view (length 420 μm), × 145. Figs 45a–b, paratype AMNH FT-1293C; a, axial view (length 380 μm), × 170; b, terminal view, × 270.

DESCRIPTION EMENDED. Test walls and septa of microgranular calcite, with little or no adventitious agglutinated material present. In thin section, there are very thin innermost and outermost layers of the walls and septa which are optically denser, and appear darker, than the principal, main thickness (analogously to the inner and outer tectoria of some Fusulinina); this could be due to the inner and outer linings of the walls and septa being composed of exceptionally small microgranules adjacently to their inner and outer surfaces. In the main mass of the walls and septa of early chambers, the calcareous microgranules appear to be randomly arranged, but in later chambers they may become protocanaliculate, and, in the last-formed chambers, canaliculi are developed regularly between these alignments.

The trochospiral test is quadriserial throughout much or all of its ontogeny. It is subcircular in equatorial section; in axial section it is subconical in shape, initially tapering at about 70°–80°, but later this appears to reduce to 30°–40° as the chambers enlarge less rapidly. The chambers are about three times as broad as high. The septa are composed of the terminal face of a chamber with the addition of the basal layer of the next, succeeding chamber: the basal layer is a quarter (or less) as thick as the preceding terminal face. In total, the septa are about a quarter to a third as thick as the chambers are high. The chambers constitute the outer third of the test diameter; the central third of the equatorial diameter is umbilical. The aperture is interiomarginal, umbilical and slit-like, being covered by a broad, plate-like lip; the lip is initially as thick as the septum from which is arises, but it thins rapidly away from the aperture which it covers; it then extends over the central, umbilical, third of the test equatorial diameter. Both the septa and the apertural lip are convex, but the latter is relatively strongly depressed, so that the umbilical area of the terminal faces of the test is in a marked depression.

REMARKS. In thin sections (Figs 47, 54), kindly sent to us by M. Septfontaine, of limestone samples obtained by him from the type level and locality of 'Valvulina' lugeoni, the species is clearly seen to be quadriserial in the adult. This coiling mode, alone, excludes it from the Cenozoic, fully triserial genus, Valvulina. The walls of true Valvulina are also fully canaliculate; these strict topotypes of Redmondoides lugeoni (Septfontaine) also show the canaliculation of the walls of the last-formed chambers and the solid walls of earlier ones – the intermediate chambers, though still solid, showing the linearity of the constituent granules which we term 'protocanaliculation' (Figs 48, 51).

STRATIGRAPHIC DISTRIBUTION. The type specimens were obtained by Septfontaine (1977) from the Grange Chavan, Préalpes valaisannes, SW of Chablais (Haute-Savoie, France),

in the upper part of the 'Couches à Mytilus' of Bathonian–Callovian age (Baud et al. 1989: 372). Furrer & Septfontaine (1977) recorded the species from sediments precisely dated as Upper Bathonian (and also possibly older) in an adjacent region. Septfontaine (1988: 238, 248) later believed 'Valvulina' lugeoni to have its first stratigraphic appearance in the Lower Dogger (in the Bajocian, and possibly even in the Aalenian) in the Mesogean Realm. We have found it in beds probably as old as Bajocian (the Izhara Formation) drilled subsurface, off-shore Abu Dhabi (Fig. 78, p. 141). In the Préalpes briançonnaise, the Callovian marine sediments are closed by a major, regional disconformity (Baud et al. 1989), and this may be responsible for the absence of post-Callovian records of Redmondoides lugeoni in that area.

Conspecific specimens were illustrated by Bayliss (1966) from the Bau Limestone Formation of western Sarawak, a formation which also contained Pseudocyclammina maynci Hottinger (illustrated by Bayliss and recorded by him as 'P. lituus (Yokoyama) form α Maync'), a species which also occurs in the 'couches à Mytilus' of the Préalpes (Hottinger 1967), as well as in beds believed to range Callovian–Oxfordian in the High Atlas of Morocco (Brun 1963). However, the Bau Limestone was also found to contain Torinosuella peneropliformis (Yabe & Hanzawa) and Pseudocyclammina lituus (Yokoyama) (Bayliss 1966), suggesting that the formation ranges up into the Kimmeridgian; therefore, the youngest occurrences here of Redmondoides lugeoni may also be as young as this.

Genus *RIYADHOIDES* nov.

TYPE SPECIES. *Pseudomarssonella mcclurei* Redmond, 1965.

DIAGNOSIS. A chrysalidinid with an initially quadriserial test reducing to adult triseriality; adult primary aperture interiomarginal, central in position; no apertural flap, no umbilicus or internal, umbilical pillars, no areal, accessory apertures; terminal faces and septa are flattened.

NAME. From Riyadh, capital city of Saudi Arabia.

REMARKS. As in *Riyadhella*, the triserial terminal whorls of *Riyadhoides* consist of chambers so closely appressed that no umbilical space can exist between them. This applies not only to the slender tests of *R. mcclurei* but also to the conical, more rapidly tapering tests of *R. dumortieri* (Schwager), which has been clearly illustrated from the Kimmeridgian – Lower Tithonian by Riegraf & Luterbacher (1989: pl. 2, figs 1–8).

The reduction during ontogeny in the number of chambers

Figs 46–54 *Redmondoides lugeoni* (Septfontaine), metatypic topotypes, random thin sections in micritic limestone, sample Se785, from the upper part of the *Mytilus* Beds, Bathonian or Callovian, at Grange Chavan, Préalpes valaisannes, near Chablais, Haute-Savoie, France. Fig. 46, BMNH P 52610, off-centred axial section (length 600 μm), showing canaliculi in walls and septa (with protocanaliculation in the umbilical area), × 110. Fig. 47, BMNH P 52612, equatorial section (breadth 1300 μm), showing partially protocanaliculate or canaliculate chamber walls, × 45. Fig. 48, BMNH P 52613, axial section (length 1260 μm), × 70. Fig. 49, BMNH P 52614, off-centred axial section (length 1280 μm), showing protocanaliculate or canaliculate terminal septum and the final, basal layer separating from its underlying (penultimate) septum, × 45. Fig. 50, BMNH P 52615, axial section, slightly oblique (length 1400 μm), × 35. Fig. 51, BMNH P 52616, axial section (length 2030 μm), showing broad, plate-like, apertural lips, × 35. Fig. 52, BMNH P 52611, axial section (length 620 μm), × 80. Fig. 53, BMNH P 52617, off-centred, axial section of terminal whorls (breadth 910 μm), showing canaliculate chamber walls and solid septa, × 75. Fig. 54, BMNH P 52618, equatorial section (breadth 1260 μm), showing quadriseriality and partially protocanaliculate chamber walls, × 45.
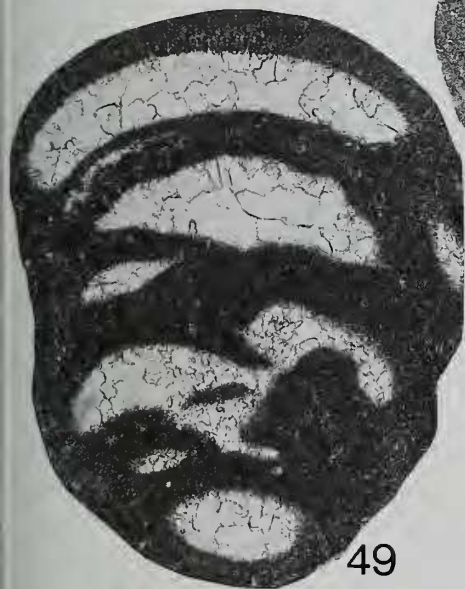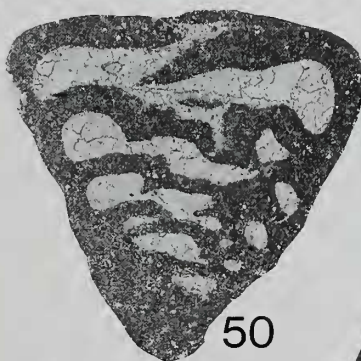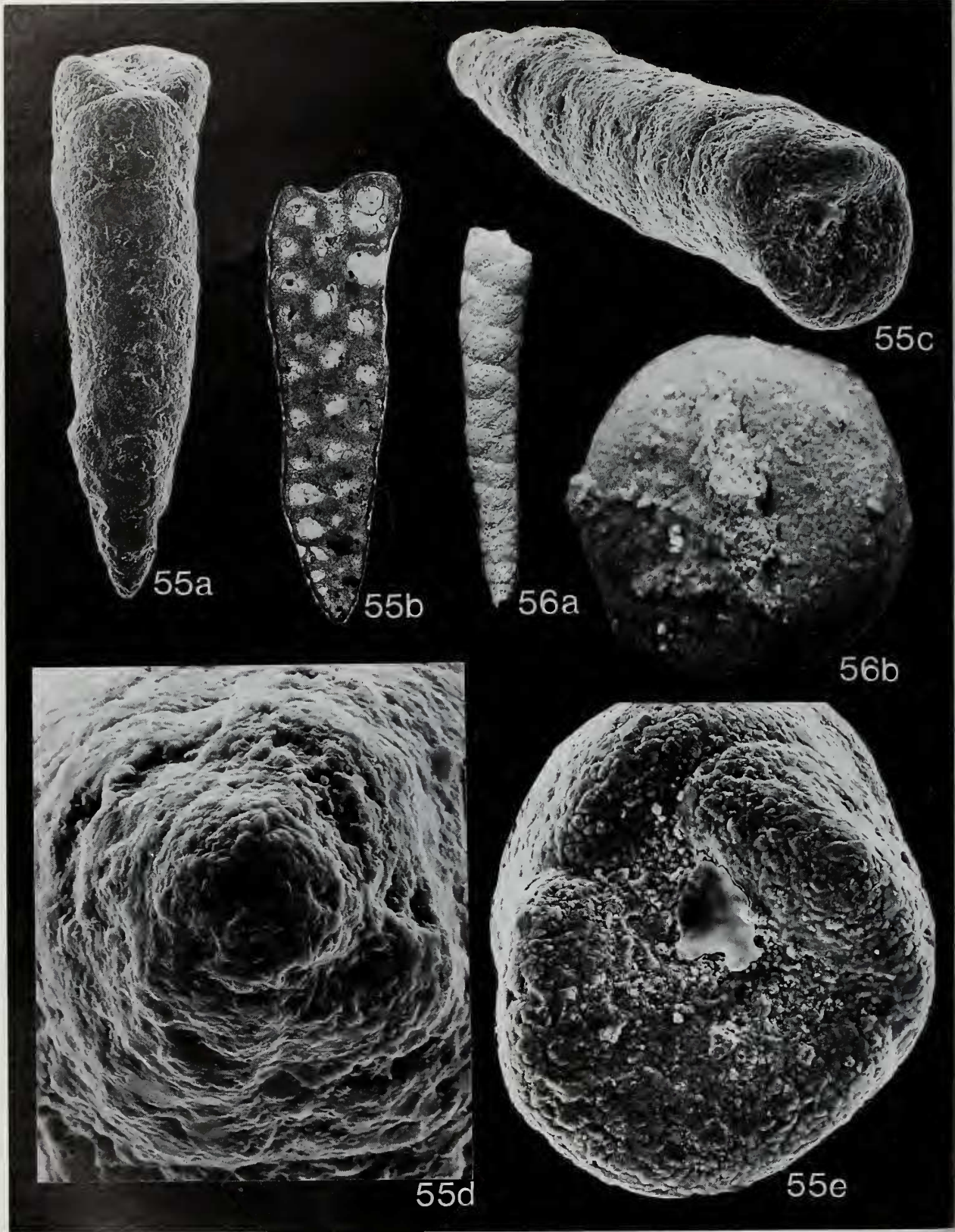
55a

55b

56a

55c

56b

55d

55e
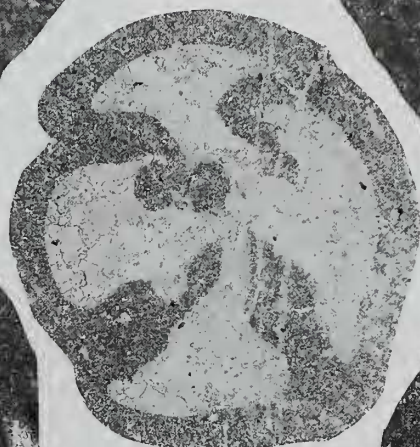
er whorl may be so great that the test can approach biseriality; however, true biseriality is not achieved. It is possible, but cannot yet be demonstrated, that further reduction in terminal chamber numbers, to achieve true biseriality, involved *Protomarssonella* Desai & Banner near the beginning of the Cretaceous.

DIFFERENTIATION AND AFFINITY. *Redmondoides*, presumed ancestor of *Riyadhoides*, differs in its quinqueserial–quadriserial coiling, as well as in possessing an umbilicus over which apertural flaps may develop. *Riyadhoides* differs from *Protomarssonella* in lacking terminal biseriality. It may be distinguished easily from *Riyadhella* Redmond by its flattened terminal faces (and septa), which form distinct angles with the uninflated chamber walls.

Riyadhoides mcclurei (Redmond, 1965)   Figs 55–56

1965   *Pseudomarssonella mcclurei* Redmond: 135; pl. 1, figs 8–10.

DESCRIPTION EMENDED. Test calcareous, microgranular, with no known canaliculi or protocanaliculate structure. The initial quadriserial part of the test is tapering, but the adult triserial part is slender, subcylindrical and nearly parallel-sided. The chamber walls are uninflated and the intercameral sutures are only narrowly and shallowly depressed. The intercameral septa are virtually perpendicular to the chamber wall, as the terminal faces of the septa are flattened or are only very slightly convex. The interiomarginal, slit-like aperture is situated in a deep re-entrant in the high apertural face and is centrally placed, in the margin of a narrow, empty umbilicus.

PROVENANCE OF TYPES. The type specimens were obtained by Redmond (1965) from the Riyadh Water Well 180 (24°37'27"N, 6°41'40"E) at 2421–2431 ft depth (ditch sample), Middle Dhruma Formation.

STRATIGRAPHY. Believed by Redmond (1965) to be rare in the lower part of the Middle Dhruma Formation, the species was referred by him to the Bathonian. Powers (1968) recorded the species as characterizing a zone in the lowest unit (Unit 5), the *Thambites* Zone limestone, of the Middle Dhruma ('?Lower Bathonian'), but Enay *et al.* (1987) called this unit 'D3' and assigned it to the latest Bajocian.

Genus *RIYADHELLA* Redmond, 1965

TYPE SPECIES. *Riyadhella regularis* Redmond, 1965.

1972   *Eomarssonella* Levina: 101 (type species *E. paraconica* Levina, 1972)

1988   *Pseudoeggerella* Septfontaine: 246 (type species *P. elongata* Septfontaine, 1988).

DIAGNOSIS. A chrysalidinid with an initially quinqueserial or quadriserial test, reducing to adult triseriality; primary aperture interiomarginal, central in position; no apertural flap, no umbilicus or internal, umbilical pillars; no areal, accessory apertures; terminal faces and septa are convex.

REMARKS. The adult reduction to triseriality in *Riyadhella* results in the production of tests which are terminally very slowly tapering or even parallel-sided. They differ from the similarly-shaped *Riyadhoides* in their highly convex septa (and chamber terminal faces) which have no trace of angularity at the junction between them and the adjacent chamber walls.
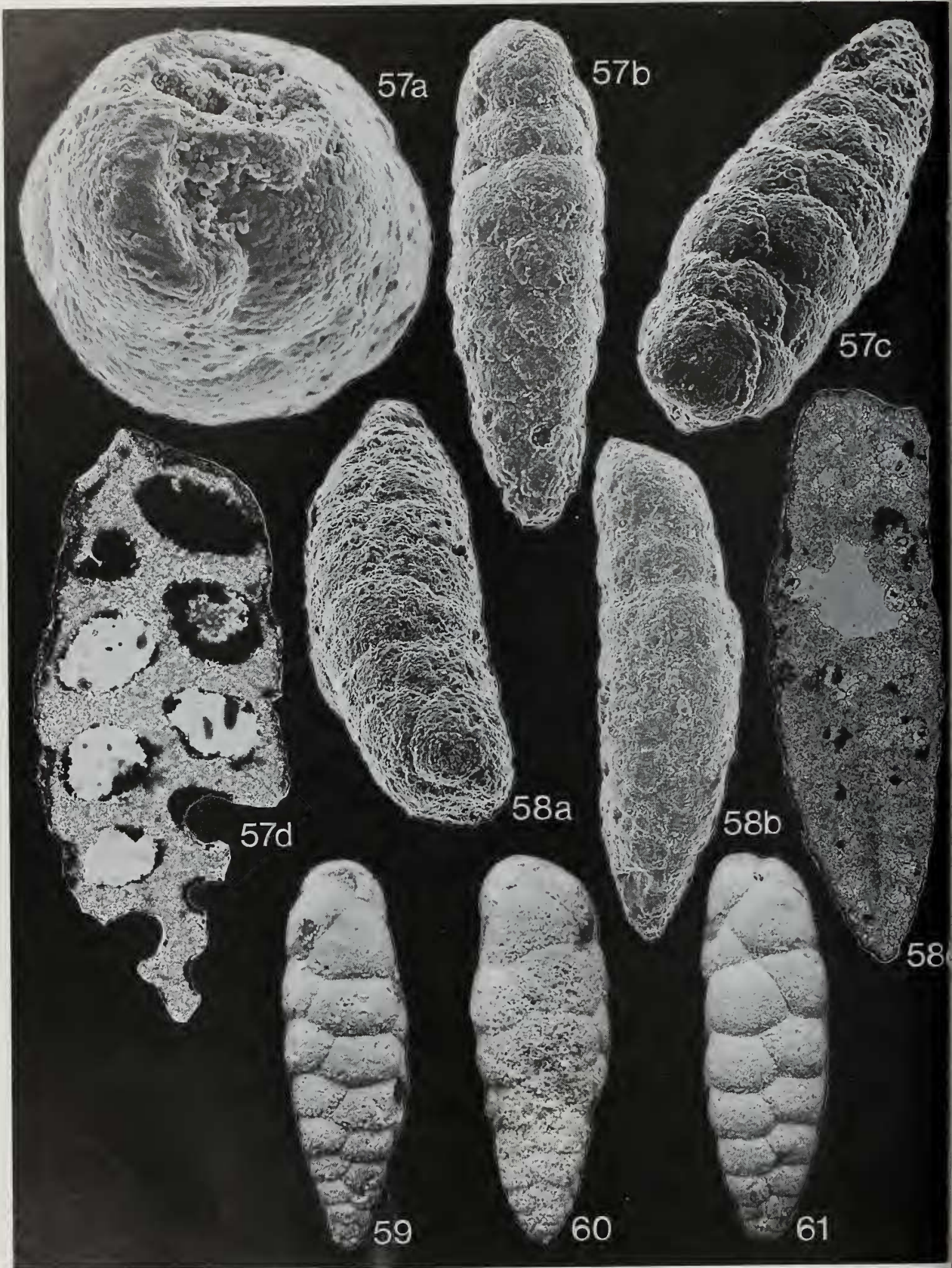
Redmond's species of *Riyadhella* were known to him only as solid specimens from the Late Bajocian and Bathonian of Saudi Arabia. Some of these specimens have now been sectioned (Figs 57–58, 63) and can be directly compared with the published photographs of the type specimens of *Pseudoeggerella* Septfontaine, which was known only as random thin sections of specimens in microfossiliferous, Bathonian limestones of Switzerland. Septfontaine (1988: 246) believed that adult *Pseudoeggerella* was quinqueserial, but neither the holotype of the type species (originally figured by Septfontaine, 1980: pl. 1, fig. 12) nor the paratypes (figured by him in 1988) suggest this to us. The 'small protuberances' in the middle part of the sectioned chambers, also considered by Septfontaine (1988) to be significant, we ascribe to partial sections of a third (or, in the earlier test, fourth) chamber of each whorl. The 'narrow columella in the axis of the test', also mentioned by Septfontaine (1988), we believe to consist of the innermost walls of the adjacent chambers, cut slightly away from the plane of the central axis (see Fig. 58c herein); there is no umbilical axial space in the test of this genus. Therefore, we believe that *Riyadhella* and *Pseudoeggerella* are synonymous, and we also consider that *P. elongata* Septfontaine is a junior synonym of *R. regularis* Redmond. In consequence, the genera may be regarded as subjective typonyms and *Riyadhella elongata* (Septfontaine, 1988) becomes a junior synonymous homonym of *R. elongata* Redmond, 1965.

Eomarssonella paraconica Levina, the type species of that genus, was described and figured by Levina (1972: pl. 32, figs 1–11; see also those figures reproduced by Loeblich & Tappan, 1988: pl. 140, figs 9–12) from the Oxfordian of western Siberia. Although some specimens (e.g. Levina 1972: pl. 32, fig. 1a) may have abnormally inflated chambers in the last whorl only, the shape of the earlier test (like the complete tests of other specimens) is indistinguishable from typical *Riyadhella*; the megalospheric form has four chambers in each early whorl, reducing to adult triseriality, the septa are highly and smoothly convex, and there is no open umbilicus. It is possible that *R. paraconica* is a junior synonym of *R. inflata* Redmond, or is, at least, closely related to it.

DIFFERENTIATION AND AFFINITY. *Riyadhella* differs from *Redmondoides* gen. nov. by its highly convex chambers, in which the terminal faces and lateral walls blend in a smooth curve with no angular junction, in its adult triseriality and in its lack of an umbilicus. It differs from *Verneuilinoides* Loeblich & Tappan by its initial quadriseriality.

STRATIGRAPHY. Named species of *Riyadhella* are known from late Bajocian (*R. elongata* Redmond), to Callovian (e.g. '*R. hemeri*' Redmond, considered to be a synonym of *R. regularis*

Figs 55–56   *Riyadhoides mcclurei* (Redmond), from Saudi Arabia, Riyadh Water Well-180, 2421–2431 ft depth, Middle Dhruma Formation, uppermost late Bajocian. Figs 55a–e, paratype AMNH FT-1272, now sectioned; a, original axial view (length 500 μm), × 200; b, axial section, × 160; c, oblique terminal view, × 250; d, initial view, × 2000; e, terminal view, × 600. Figs 56a–b, holotype AMNH FT-1271; a, axial view (length 940 μm), × 70; b, terminal view, × 600.

Redmond) and to Oxfordian (*R. paraconica*). Unnamed species of *Riyadhella* are known to us, in random thin section, in the Kimmeridgian Arab Zone ('C' Zone) limestone of Qatar. The genus is known only from the mid and late Jurassic, and so differs from its presumed ancestor, *Verneuilinoides*, which ranges from early Jurassic to Cretaceous.

Riyadhella regularis Redmond, 1965   Figs 57–63

1965   *Riyadhella regularis* Redmond: 138–140; pl. 1, figs 32–34.

1965   *Riyadhella hemeri* Redmond: 137; pl. 1, figs 23–24.

1965   *Riyadhella intermedia* Redmond: 137–138; pl. 1, figs 25–27.

1965   *Riyadhella nana* Redmond: 138; pl. 1, figs 28–31.

1980   '*Pseudoeggerella*' Septfontaine: 181–182; pl. 1, fig. 12.

1988   *Pseudoeggerella elongata* Septfontaine: 246; pl. 2, figs 6–8.

DESCRIPTION EMENDED. Walls and septa of microgranular calcite, with little or no adventitious agglutinated material; no protocanaliculation or canaliculi are known. The nepionic test is quadriserial, but the neanic and ephebic parts of the test are regularly triserial. The test is subcircular in cross-section; in axial view, the test initially tapers at about 25°–40° but soon becomes approximately parallel-sided. The chambers are about as high as broad, but those of successive whorls embrace the preceding ones for about a third to half of their height. The intercameral sutures are weakly depressed; the surfaces of both walls and terminal faces are smooth. The terminal faces of the chambers (and the septa of earlier chambers) are highly convex. In longitudinal section, the thickness of each septum is about a quarter of the total height of its chamber. The apertural face is low, flattened but otherwise ill-defined, containing a deep re-entrant depression in which is situated the narrow, short, interiomarginal, slit-like aperture.

REMARKS. Redmond (1965) considered that the test of *Riyadhella regularis* had an initial part which was more elongately conical than the 'blunter' initial end of *R. intermedia*. Neither Redmond's published pictures (1965: pl. 1, figs 25–27 and 32–34) nor our SEM images (Figs 57–60) substantiate this. Also, Redmond (1965) considered that these taxa had 'relatively straight sides', while *R. nana* and *R. hemeri* were distinguished by being broader medially, the former having its widest diameter closer to its 'apex' than in the latter. The test of *Riyadhella* is often broadest at the last quadriserial whorls (the succeeding triserial whorls being often, but not always, slimmer); the relative position in the test of this event depended on the extent of triserial chamber

growth which had been achieved. These differences are both minor and unsystematically developed. Consequently, we consider all these taxa to be synonyms, and (by ICZN Art. 24) as first revisers we select *R. regularis* (designated by Redmond, 1965, as the type species) to have priority.

DIFFERENTIATION. *Riyadhella regularis* Redmond is much broader than *R. elongata* Redmond, a species which also remains quadriserial for at least half of the length of its elongate test: in *R. regularis*, quadriseriality is retained only for a quarter, or less, of the length of the adult test. *R. arabica* Redmond and *R. inflata* Redmond are broader and more tapering and have more broadly inflated chambers.

PROVENANCE OF TYPES. The type specimens of *Riyadhella regularis* (Figs 57, 59) came from Aramco well T 60A (24°55′04″N, 45°59′08″E), 40–60 ft depth, basal member of the Upper Dhruma Formation. Of the synonyms, the *R. nana* type specimens (Figs 62–63) came from the same well, but from 100–105 ft depth, the upper part of the Middle Dhruma Formation. The holotype (there were no paratypes) of *R. hemeri* (Fig. 61) came from Aramco surface locality (outcrop) C-3 (24°12′48″N, 46°21′20″E), 'shale approximately 51 metres below the base of the cliff-forming limestone of the Tuwaiq Mountain Formation' (Redmond 1965: 140), which Powers (1968) referred to the Hisyan (Hishyan) Member of the uppermost Dhruma Formation. The type specimens of *R. intermedia* (Figs 58, 60) were obtained from the same shale member, about 25 m below the Tuwaiq Mountain Formation limestone, at Aramco surface (outcrop) locality L 930A (sample 32) (24°10′50″N, 46°27′53″E).

STRATIGRAPHY. *Riyadhella nana* was obtained primarily from beds referred by Powers (1968) to the *Dhrumaites* Zone, 'Unit 8' of the uppermost Middle Dhruma, beds which were relabelled 'D6' by Enay *et al.* (1987) and considered by them to be mid or late Bathonian. *R. regularis* was recorded as 'common in the basal member of the Upper Dhruma' (Redmond 1965) which was called the 'Atash Member ('Unit 9') by Powers (1968); Enay *et al.* (1987), who called the member 'D7a', considered it to be late Bathonian or early Callovian in age, but they had no direct palaeontological evidence. *R. hemeri* and *R. intermedia*, from the Hisyan Member ('D7b') were mid Callovian by the stratigraphy of Enay *et al.* (1987), who also considered the overlying Tuwaiq Mountain Formation to be mid Callovian in age. The species is therefore known to range from mid or late Bathonian to mid Callovian, and Septfontaine's specimens (1980, 1988) are believed to have come from the Bathonian part of this range.

Figs 57–61   *Riyadhella regularis* Redmond, from Saudi Arabia. Figs 57a–d, paratype of *R. regularis* AMNH FT-1291, now sectioned; from Aramco Well T 60A, 40–60 ft depth, basal Upper Dhruma Formation, 'Atash Member, late Bathonian or early Callovian; a, terminal view, × 600; b, axial view (length 360 μm), × 250; c, oblique axial view, × 300; d, axial section, × 385. Figs 58a–c, paratype of the synonymous *R. intermedia* Redmond, AMNH FT-1287, now sectioned; from Aramco outcrop L 930A, Hisyan Member, Upper Dhruma Formation, mid Callovian; a, oblique axial view, × 250; b, axial view (length 460 μm), × 200; c, axial section, × 225. Fig. 59, holotype of *R. regularis* AMNH FT-1290, from same sample as paratype (Fig. 57); axial view (length 420 μm), × 165. Fig. 60, holotype of the synonymous *R.intermedia* Redmond, AMNH FT-1286, from the same sample as its paratype (Fig. 58); axial view (length 440 μm), × 160. Fig. 61, holotype of the synonymous *R. hemeri* Redmond, AMNH FT-1283, from Aramco outcrop C-3, Hisyan Member, Upper Dhruma Formation, mid Callovian; axial view (length 450 μm), × 155.
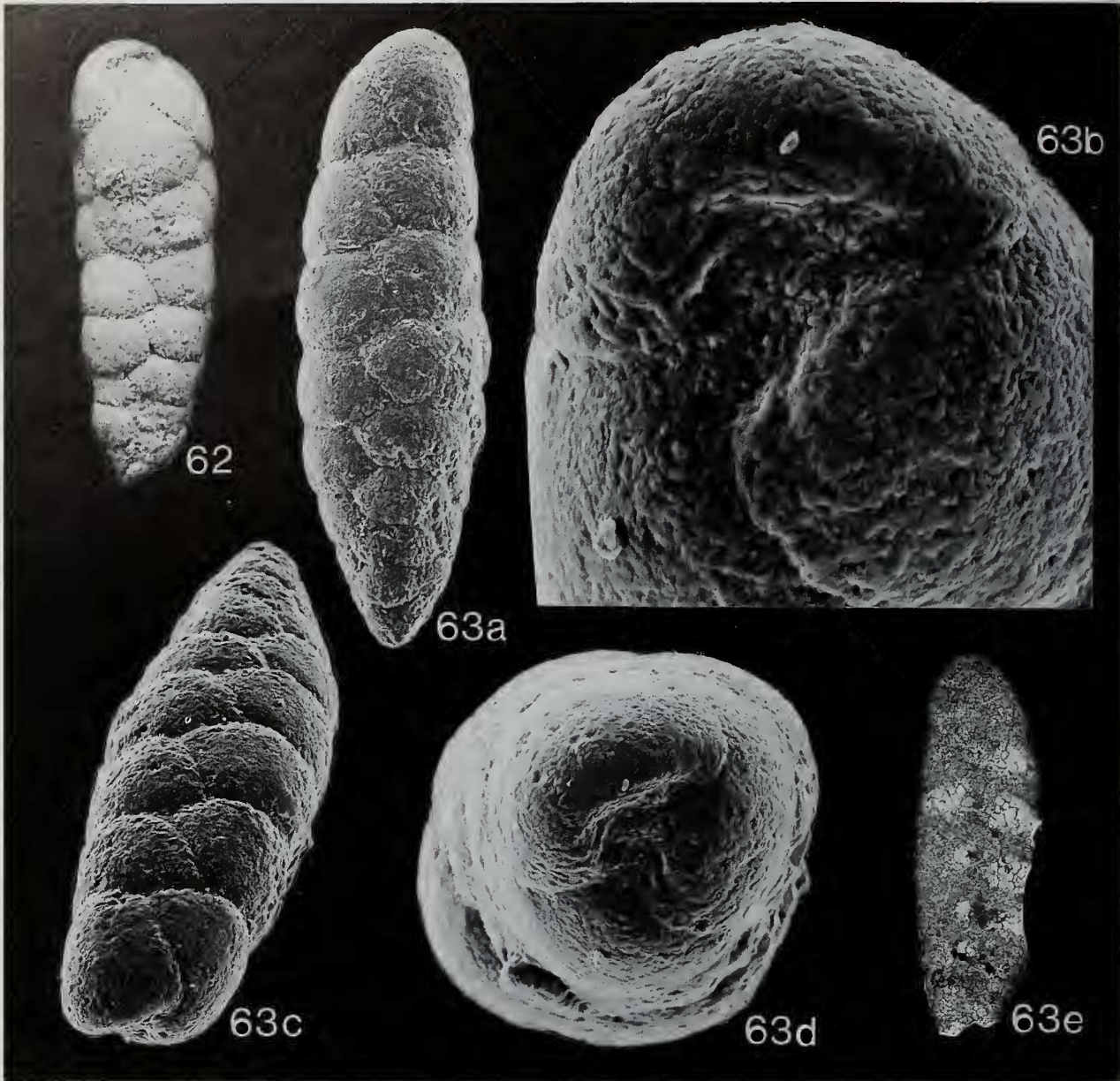
Figs 62–63 *Riyadhella regularis* Redmond; primary types of the synonymous *R. nana* Redmond, from Saudi Arabia, Aramco Well T 60A, 100–105 ft depth, upper Middle Dhruma Formation, mid or late Bathonian. Fig. 62, holotype of *R. nana*, AMNH FT-1288; axial view (length 370 μm), × 190. Figs 63a–e, paratype of *R. nana*, AMNH FT-1289, now sectioned; a, original axial view (length 390 μm), × 250; b, apertural view, × 1,000; c, oblique axial view, × 300; d, terminal view, × 500; e, axial section, × 160.

Riyadhella arabica Redmond, 1965   Fig. 66

1965 *Riyadhella arabica* Redmond: 136; pl. 1, fig. 35.

REMARKS. Only the holotype of this taxon was deposited by Redmond in the American Museum of Natural History, so the species cannot properly be redescribed. Also, the aperture is obscured on the holotype by a coating of calcareous sediment. However, the holotype is much bigger than the specimens referred here to *R. regularis*, more broadly tapering (initially at about 40°–45°) and does not clearly become parallel-sided in the adult. The chambers are smooth-walled, weakly inflated, and are about as high as broad; successive whorls embrace previous ones by about half the chamber height. *R. inflata* Redmond has much higher chambers, and in that species successive whorls embrace previous ones by about a quarter of the chamber height.

The type specimen of *R. arabica* Redmond came from Riyadh Water Well 1, at 2355–2360 ft depth – the same sample as that from which the type specimens of *R. elongata* Redmond were obtained – and Redmond (1965) reported
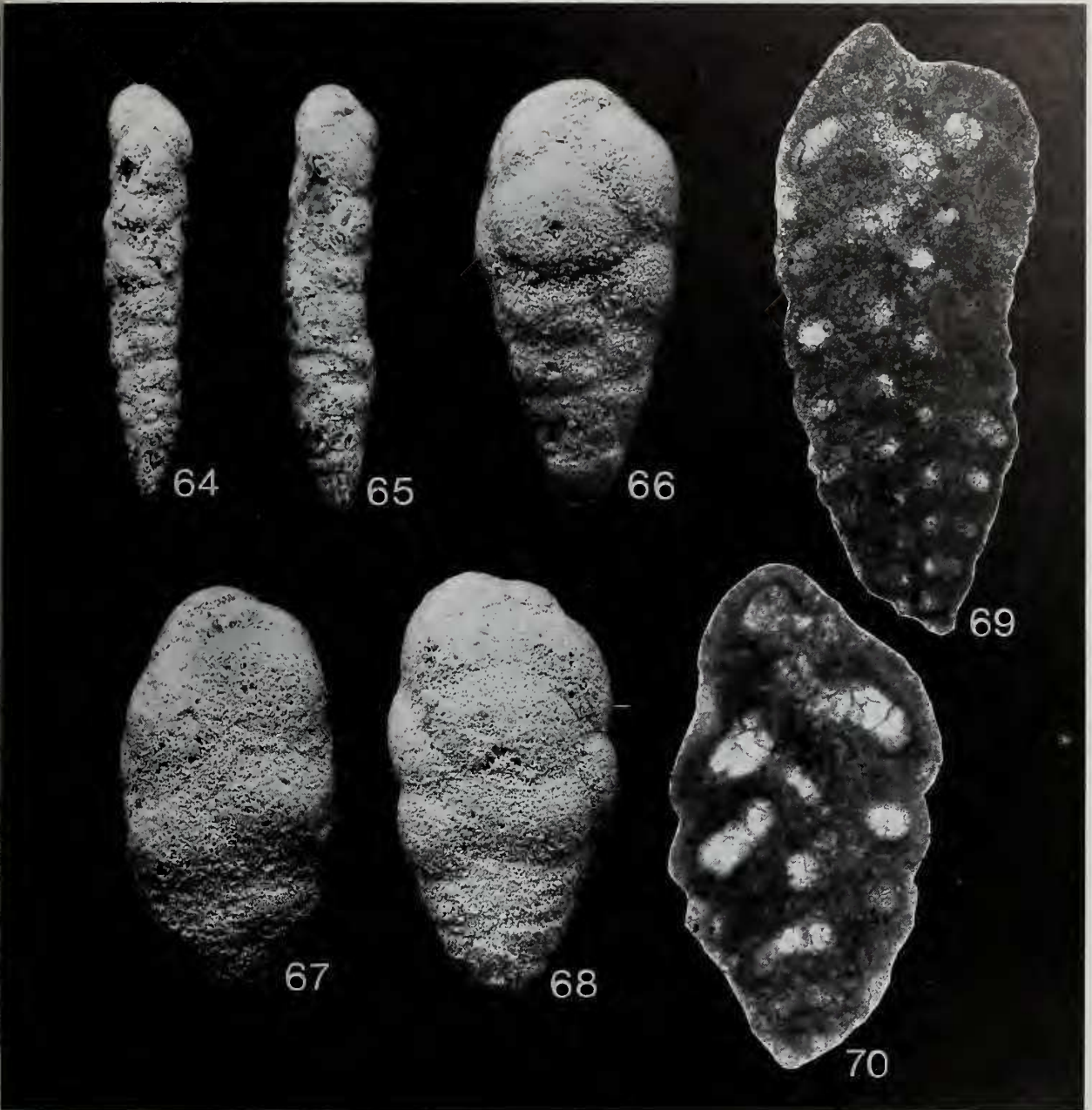
Figs 64–65 *Riyadhella elongata* Redmond, from Saudi Arabia, Riyadh Water Well-1, 2350–2360 ft depth, Middle Dhruma Formation, early Bathonian. Fig. 64, holotype AMNH FT-1281, axial view (length 450 µm), × 145. Fig. 65, paratype AMNH FT-1282, axial view (length 440 µm), × 150.

Fig. 66 *Riyadhella arabica* Redmond, from Saudi Arabia, Riyadh Water Well-1, 2355–2360 ft depth, Middle Dhruma Formation, early Bathonian; holotype AMNH FT-1280, axial view (length 400 µm), × 170.

Figs 67–68 *Riyadhella inflata* Redmond, from Saudi Arabia, Aramco Well T 80, 60–70 ft depth, Middle Dhruma Formation, mid or late Bathonian. Fig. 67, holotype AMNH FT-1284, axial view (length 610 µm), × 110. Fig. 68, paratype AMNH FT-1285, axial view (length 610 µm), × 110.

Figs 69–70 *Riyadhella* spp. from Iraq, Wadi Amij Well, depth 570–573 ft (same locality and depth as for the holotype of *Amijiella amiji* (Henson); called '?*Verneuilina* sp.' by Henson, MS), probably Bathonian, Muhaiwir Formation. Fig. 69, BMNH P 52619, axial section (length 690 µm), × 140. Fig. 70, BMNH P 52620, axial section (length 560 µm), × 140.

that this species was 'rare in the middle and lower parts of [the] middle Dhruma Formation'. Enay *et al.* (1987) would refer this interval to the early Bathonian.

It is possible that *R. arabica* Redmond is a distinct species, as its holotype appears to be morphologically distinct from the type specimens of the other taxa, and Redmond's (1965) treatment may prove to have been correct.

Riyadhella elongata Redmond, 1965   Figs 64–65

1965   *Riyadhella elongata* Redmond: 136–137; pl. 1, figs 20–21.

DESCRIPTION EMENDED. Walls and septa of microgranular calcite, with scattered fine quartz particles in the walls, which roughen the chamber surfaces; no protocanaliculation or canaliculi are known. The nepionic and neanic parts of the test are quadriserial but triseriality is attained in the ephebic stage. The test is subcircular in cross-section; initially, it tapers at about 30° but it becomes parallel-sided and slender during late quadriseriality and this is maintained during triseriality, so that the adult test is 4½–5 times as long as broad. The chambers are about as high as broad, but those of successive whorls embrace the preceding ones for about a third to half of their height. The intercameral sutures are distinctly depressed, and the walls are inflated; the terminal faces are highly convex. The apertural face is low, and the short, interiomarginal aperture is set in a broad re-entrant depression.

DIFFERENTIATION. *Riyadhella elongata* Redmond is easily recognized by its thin, parallel-sided test, which Redmond (1965) called 'needle-like', and its ontogenetically late development of triseriality.

PROVENANCE OF TYPES. The type specimens were obtained from the Riyadh Water Well 1 (24°37'45"N, 46°41'06"E) at 2350–2360 ft depth, Middle Dhruma Formation.

STRATIGRAPHY. Redmond (1965) reported that *R. elongata* first occurred in the 'uppermost part of [the] lower Dhruma', an occurrence recorded by Powers (1968) who placed it in his 'Unit 4', the Dhibi Member (*Ermoceras* Zone) of the Lower Dhruma; this was relabelled 'Unit D2' by Enay *et al.* (1987), who believed it to belong to the earliest late Bajocian. These are the stratigraphically earliest records yet of *Riyadhella*. Redmond (1965) also believed *R. elongata* to be 'rare in middle and lower part of middle Dhruma Formation', occurrences which were noted by Powers (1968) in his 'Unit 6' (*Tulites* Zone) and 'Unit 7' (*Micromphalites* Zone) of the middle Middle Dhruma; Enay *et al.* (1987) renamed these units 'D4' and 'D5' and believed both to comprise the Lower Bathonian. Therefore, *R. elongata* is believed to range from the earliest Late Bajocian to the latest early Bathonian.

Riyadhella inflata Redmond, 1965   Figs 67–68

1965   *Riyadhella inflata* Redmond: 137; pl. 1, figs 23–24.
?1972   *Eomarssonella paraconica* Levina: 102–104; pl. 32, figs 1–11.

DESCRIPTION EMENDED. The test is of microgranular calcite (with little or no adventitious agglutinated material) with a smooth surface; no protocanaliculation or canaliculi are yet known. The nepionic test is quadriserial, but triseriality is achieved in the neanic and ephebic stages. The test is subcircular in cross-section. In axial view, the test initially tapers broadly (at about 70°) and then more narrowly (at about 50°), becoming nearly parallel-sided in the adult. The chambers are about as high as broad, and those of successive whorls embrace those of preceding whorls by a quarter, or less, of their height. The chamber walls are weakly inflated and the intercameral sutures are distinctly and smoothly depressed. The terminal faces are highly convex. The apertural face is very low, and slightly flattened and oblique to the longitudinal axis of the test; the short aperture is interiomarginal and set at the base of a narrow, shallow depression in the apertural face.

DIFFERENTIATION. The test is much larger (thicker and proportionately longer) than any other known species of *Riyadhella*, and its chambers are higher and less embraced by succeeding whorls. The chambers are more evenly inflated, and the intercameral sutures are more smoothly, more evenly depressed. *R. paraconica* (Levina) is very similar in general morphology but its walls may be built with more adventitious, agglutinated, terrigenous material; its identity with *R. inflata* Redmond should be checked by direct re-examination of the type specimens.

PROVENANCE OF TYPES. The type specimens of *R. inflata* Redmond came from Aramco well T 80 (24°10'50"N, 46°27'53"E), from 60–70 feet depth, a level ascribed (Redmond 1965) to the Middle Dhruma Formation.

STRATIGRAPHY AND DISTRIBUTION. Stated by Redmond (1965) to be 'common in upper part of [the] middle Dhruma Formation', *R. inflata* was recorded by Powers (1968) from the top unit ('Unit 8'), the *Dhrumaites* Zone, of the Middle Dhruma, 'middle or upper Bathonian'. Enay *et al.* (1987) renamed the unit 'D6', but also considered that it was mid or late Bathonian in age. It has not yet been recorded from any other interval.

The type specimens of *R. paraconica* (Levina) came from the Lower Oxfordian near Tyumen' (57°11'N, 65°29'E), western Siberia, and it was also recorded (Levina 1972) from the Upper Oxfordian of that region. This is the most northerly known occurrence of *Riyadhella*, and, if its synonymity with *R. inflata* is proved, it shows that that species is the longest ranging (Bathonian–Oxfordian).

Genus *PSEUDOMARSSONELLA* Redmond, 1965

TYPE SPECIES. *Pseudomarssonella maxima* Redmond, 1965.

DIAGNOSIS EMENDED. A chrysalidinid with a test which is initially quinqueserial or quadriserial, then either retaining quadriseriality throughout ontogeny or developing quinqueseriality in the ephebic stage of development; the adult

Fig. 71 *Pseudomarssonella maxima* Redmond, holotype AMNH FT-1269, from Saudi Arabia, Aramco well T 60A, 50–60 ft depth, basal Upper Dhruma Formation ('Atash Member), late Bathonian or early Callovian; a, axial view (length 630 μm), × 95; b, axial-terminal view showing canaliculate wall, × 350; c, terminal view, × 155; d, enlargement of part of last whorl (of Fig. 71a), showing canaliculi in broken chamber wall, × 475; e, apertural terminal view, × 325.

primary, interiomarginal aperture is covered by an apertural flap which fuses to the apertural flap or face of an opposing chamber, and which is penetrated by areal, accessory, cribrate, pore-like apertures; the apertural flaps of successive whorls are closely appressed and can fill the deep umbilical hollow with a layered column of successive flaps; there are no internal, umbilical pillars; the terminal faces and septa are flattened or only weakly convex, and make distinct angles with the uninflated chamber walls.

REMARKS AND DIFFERENTIATION. The broadening of the umbilicus and umbilical hollow (compared to the narrower structure

in *Redmondoides*) led to the broadening of the apertural flap and its strengthening by fusion with the surface of opposite chambers; this fusion caused loss of the interiomarginal accessory aperture and its replacement by areal accessory apertures. The increased breadth of the umbilicus led to five chambers (rather than the ancestral four) being able to surround it in some species. Successive flaps became closely appressed (even when only four chambers occupied the whorl – the acquisition of five chambers per whorl would have meant that five, not four, flaps would have been accommodated in each whorl), and cytoplasm, egressing from the chamber lumina through the areal, cribrate apertures,
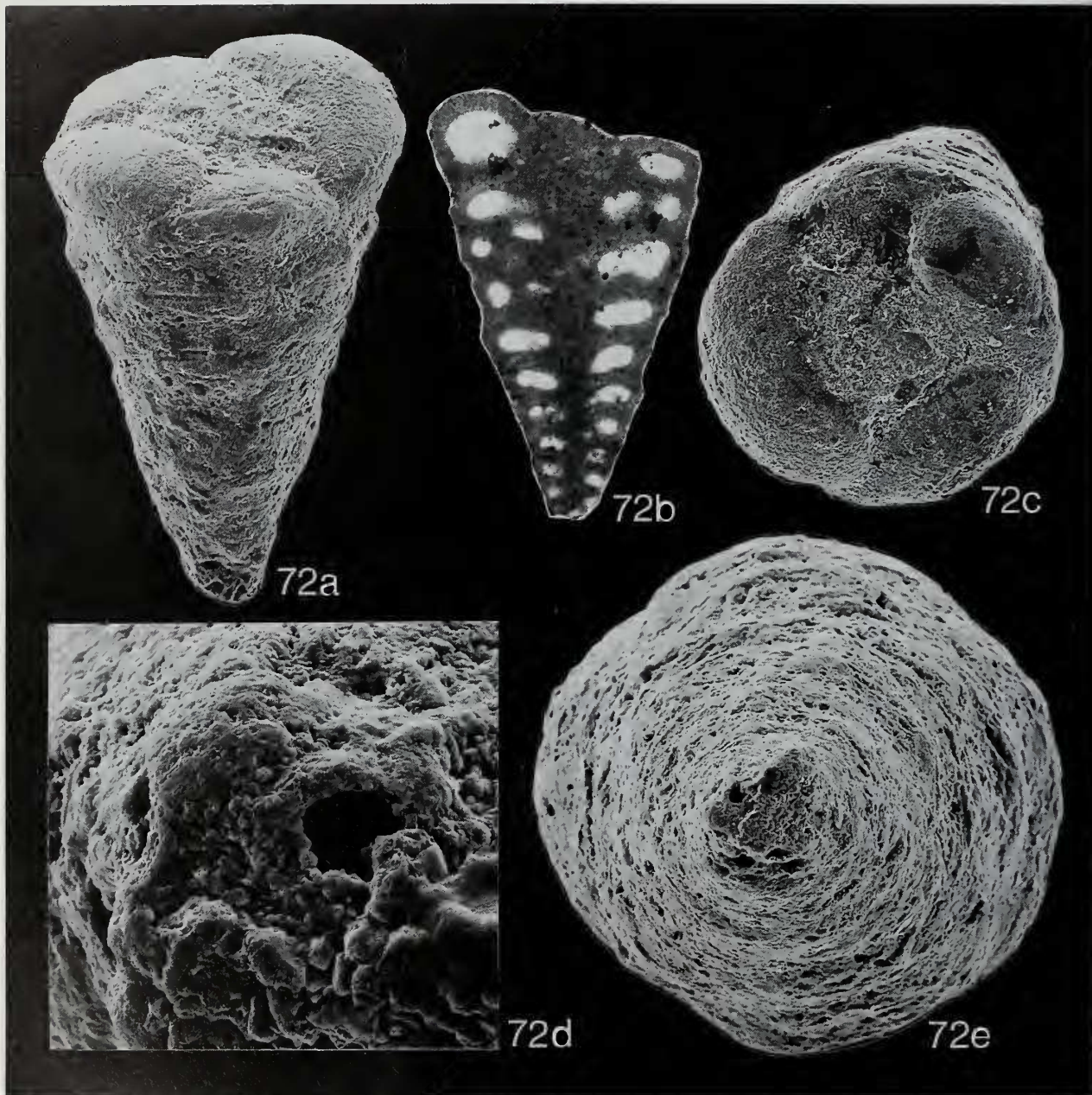
Fig. 72   *Pseudomarssonella maxima* Redmond, paratype AMNH FT-1270, from same locality and sample as holotype (Fig. 71, p. 135), now sectioned; a, original axial view (length 600 µm), × 150; b, axial section, × 115; c, terminal view, × 150; d, initial end, × 1,100; e, initial view, × 220.

would have had narrow, sheet-like channels to traverse, between the successive flaps. This may have encouraged the development of the succeeding *Paravalvulina*, where inter-flap spacing was enlarged and structural support was provided by the development of inter-flap pillars.

SPECIES INCLUDED AND STRATIGRAPHY. In addition to *Pseudomarssonella maxima* Redmond, the type species, three other nominal species, named by Redmond (1965), are retained in the genus: *P. bipartita* and *P. plicata* (with the subjective synonym of the latter, *P. reflexa*). These are redescribed below, and the revised known range for the genus is regarded as mid Bathonian to mid Callovian (following the revision of the stratigraphy by Enay *et al.*, 1987). No species firmly assignable to this genus have yet been described from deposits of western Tethys and it is so far known only from Saudi Arabia and from offshore wells of Qatar and the United Arab Emirates.

Pseudomarssonella maxima Redmond, 1965 Figs 71–72

1965   *Pseudomarssonella maxima* Redmond: 135; pl. 1, figs 6–7.

DESCRIPTION EMENDED. Test walls and septa of microgranular calcite, with little or no adventitious agglutinated material; the calcite microgranules are random in early ontogeny, but they become aligned and the walls become protocanaliculate until canaliculi can develop in the final growth stages, both in chamber walls and septa. The test may be quinqueserial nepionically but it rapidly becomes quadriserial, sometimes becoming quinqueserial again, in the final growth stage. It is subcircular in cross-section and axially it is a regularly taper-ing cone, with its sides diverging at about 40°.

The intercameral sutures are very narrowly and gently depressed or are flush with the chamber walls. The walls are uninflated and the terminal faces and septa are weakly convex, making angles of 90° or more with the walls; the angular wall–septal junctions sometimes project very slightly from the test sides. The chambers are about twice as broad as high.

The interiomarginal, umbilical primary apertures are covered by broad, flattened or slightly convex flaps which span most or all of the umbilicus to fuse with the flaps or apertural faces of opposing chambers. The flaps are penetrated by areal, cribrate, pore-like accessory apertures, each of which is circular and is usually furnished with a narrow, low, upstand-ing rim. The umbilical area is slightly concave, the umbilical flaps being flatter than, originating below and being depressed below the terminal faces of the last-formed chambers. In longitudinal section, the flaps of successive whorls of cham-bers are closely appressed, being separated by spaces no thicker than (and sometimes much thinner than) the flaps themselves. The umbilicus broadens with growth, becoming from 35% to 55% of the equatorial diameter of the test.

REMARKS. Only the holotype and one paratype were depos-ited by Redmond in the American Museum of Natural History. In order to redescribe this taxon as fully as possible, the paratype was first photographed by SEM (Figs 72a, c–e), and then longitudinally sectioned and re-photographed (Fig. 72b). The total lack of internal, intraumbilical (inter-flap) pillars serves now to distinguish *Pseudomarssonella* Redmond from *Paravalvulina* Septfontaine, taxonomically and phylo-genetically.

DIFFERENTIATION. *Pseudomarssonella maxima* differs from *P. plicata* Redmond in possessing a much broader umbilicus, with broader apertural flaps, and less depressed chamber walls and much less protruding mural–septal junctions. *P. maxima* differs from *P. bipartita* Redmond in having more convex, less flattened septa and terminal faces and in being less fully quinqueserial terminally. All three species are clearly very closely related and the differences between them may be infraspecific. However, the Aramco records (restated by Powers, 1968) of full microfossil assemblages regarded them as being taxonomically distinct, and it would be unwise to contradict this when using only a few, although type, specimens.

PROVENANCE OF TYPES. The holotype and paratype were obtained by Redmond (1965) from Aramco well (drill hole) T 60A (24°55′04″N, 45°59′08″E), at 50–60 ft depth, basal mem-ber of the Upper Dhruma Formation.

STRATIGRAPHY. Redmond (1965) stated that *P. maxima* was 'rare to common throughout basal member of [the] upper Dhruma Formation', and it was cited by Powers (1968) as occurring in the 'Atash (chalky) Member ('Unit 9'). This was relabelled 'D7a' by Enay *et al.* (1987), who considered it to be late Bathonian or early Callovian. The type specimens are therefore younger than those of *P. bipartita* Redmond (mid or late Bathonian), but are of the same age as some of those of *P. plicata* Redmond (early Bathonian to late Bathonian or early Callovian).

Pseudomarssonella bipartita Redmond, 1965
Figs 73–74

1965   *Pseudomarssonella bipartita* Redmond: 134; pl. 1, figs 2–3.
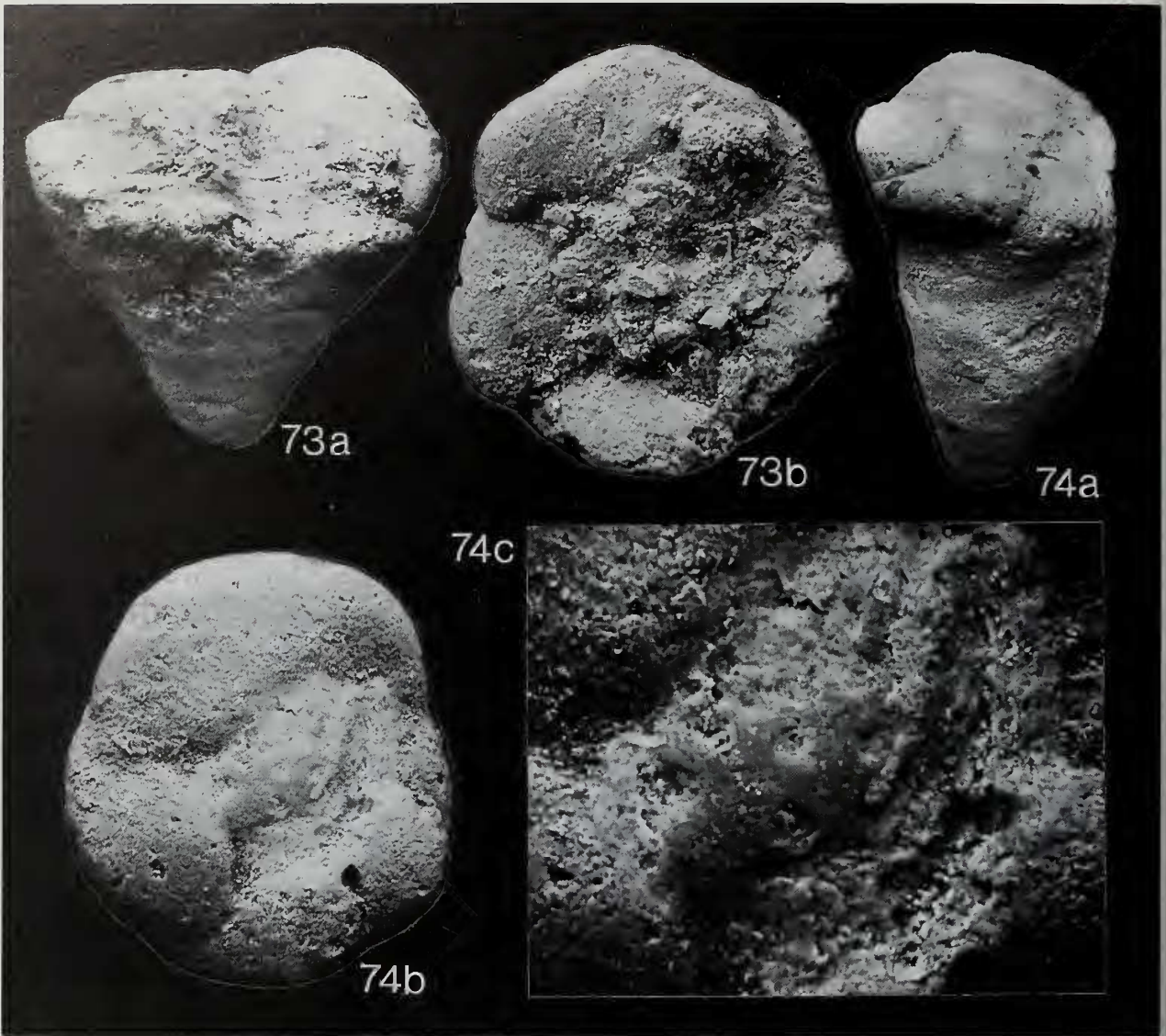non 1989   *Pseudomarssonella bipartita* Redmond; Delance & Ruget: 206; pl. 3, fig. 16.

DESCRIPTION EMENDED. Test walls and septa of microgranular calcite, with little or no adventitious agglutinated material; canaliculi are not yet known. The test may be quinqueserial nepionically, but it becomes, at least neanically, quadriserial and is ephebically and terminally quinqueserial. It is sub-circular in cross-section, and axially it is a narrowly or broadly tapering cone, tapering initially at about 40° but terminally maintaining or diminishing this angle (to about 30°) or becoming flaring (to about 70°); in all cases, five chambers constitute the last whorl.

The late chambers are about 2½ times as broad as high and constitute about 30% of the test diameter; the central 40% of the equatorial diameter is umbilical. The terminal faces of the chambers are flattened or very weakly convex, and the chamber walls are uninflated; the intercameral sutures are very narrowly depressed or flush with the chamber walls.

The interiomarginal primary apertures are covered by broad, flattened or very weakly convex flaps which span most or all of the umbilicus, to fuse with the apertural faces or flaps of the opposing chambers. The flaps are penetrated by areal, cribrate, pore-like accessory apertures. The umbilical area is slightly concave, the umbilical flaps being depressed below the terminal faces of the last-formed chambers.

DIFFERENTIATION. *Pseudomarssonella bipartita* Redmond is the only species distinctly to possess five chambers per whorl in its terminal growth stage.

Figs 73–74   *Pseudomarssonella bipartita* Redmond, from Saudi Arabia, Aramco Well T 61, 80–90 ft depth, Middle Dhruma Formation, mid or late Bathonian. Figs 73a–b, holotype AMNH FT-1265; a, axial view (length 440 μm), × 140; b, terminal view, × 140. Figs 74a–c, paratype AMNH FT-1266; a, axial view (length 560 μm), × 110; b, terminal view, × 140; c, apertural area, × 325.

REMARKS. The difference in tapering angles between the holotype (Fig. 73a) and paratype (Fig. 74a) cannot be ascribed to structural differences between the megalospheric and microspheric generations because the tapering angles of the initial parts of the tests are the same. In each case, also, the number of chambers per adult whorl is the same. Therefore, the difference must be due to an increased rate of growth (in the case of specimens like the holotype) during ephebic ontogeny, while in others (like the figured paratype) the chamber-enlargement rate remained constant or even diminished. This could have resulted from palaeoecological differences and, therefore, would not have been inherited.

The specimen figured as *P. bipartita* by Delance & Ruget (1989) is referred by us to *Redmondoides medius* (Redmond) (p. 120).

Figs 75–77   *Pseudomarssonella plicata* Redmond. Figs 75–76, primary types; from Saudi Arabia, Aramco Well T 60A, 10–20 ft depth, basal Upper Dhruma Formation ('Atash Member), late Bathonian or early Callovian. Figs 75a–b, holotype AMNH FT-1275; a, axial view (length 410 μm), × 160; b, initial view, × 270. Figs 76a–c, paratype AMNH FT-1276; a, axial view (length 350 μm), × 200; b, terminal view, × 290; c, lateral view of apertural area, × 450. Figs 77a–b, holotype AMNH FT-1279 of the synonymous *P. reflexa* Redmond, from Saudi Arabia, Aramco well 4A, 4875 ft depth, Middle Dhruma Formation, early Bathonian; a, terminal view, × 150; b, axial view (length 560 μm), × 120.
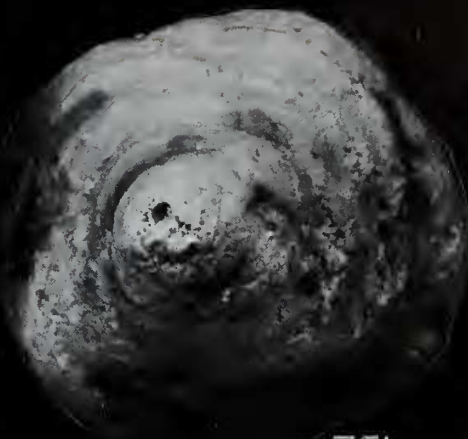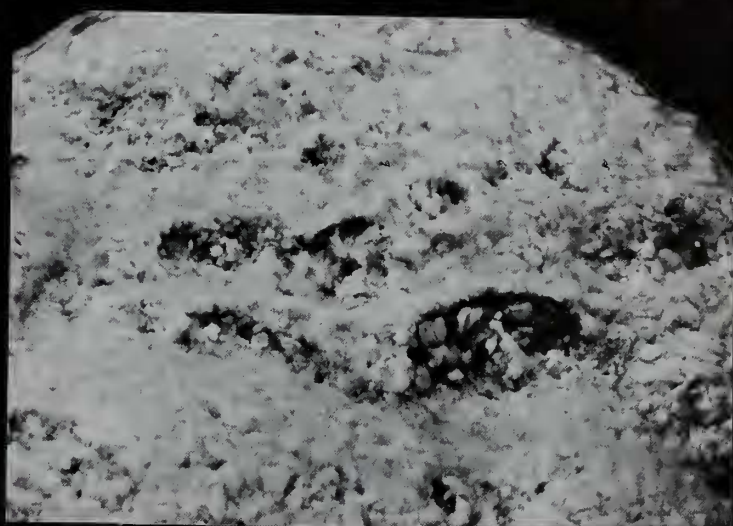
PROVENANCE OF TYPES. The type specimens of *P. bipartita* came from Aramco well T 61 (24°54′55″N, 45°58′34″E), from 80–90 ft depth, Middle Dhruma Formation.

STRATIGRAPHY. Redmond (1965) recorded *P. bipartita* as being 'rare to common in the upper part of middle Dhruma Formation', and Powers (1968) reported it from Unit 8 (the *Dhrumaites* Zone limestones and shales of the uppermost Dhruma). Enay *et al.* (1987) renamed this unit 'D6' and considered it to belong to the mid or late Bathonian.

Pseudomarssonella plicata Redmond, 1965   Figs 75–77

1965   *Pseudomarssonella plicata* Redmond: 135; pl. 1, figs 14–15.
1965   *Pseudomarssonella reflexa* Redmond: 136; pl. 1, figs 19a–b.

DESCRIPTION EMENDED. Test walls and septa of microgranular calcite, with little or no adventitious agglutinated material; canaliculi are not yet known. The test may be quinqueserial nepionically, but it is quadriserial for most, at least, of its growth; it is subcircular in equatorial section, and axially it is conical, tapering steadily at 40°–50°.

The chambers are about three times as broad as high, and constitute the outer 35% of the test diameter; the central 30% of the equatorial diameter is umbilical. The terminal faces of the chambers are only very weakly convex, while the chamber walls are uninflated; the walls and the terminal faces meet at distinct but obtuse angles. The intercameral sutures are flush or very narrowly depressed, but may be marked by the slight protrusion of these angular mural–septal junctions.

The interiomarginal primary apertures are covered by broad flaps which arise from low on the apertural face to extend to and fuse with the lower part of the apertural face of the opposite chamber; the accessory apertures are multiple, cribrate, pore-like and emerge through the area of the flaps; each accessory aperture is subcircular and is bounded by a weakly elevated rim. The umbilical area is slightly concave, the umbilical flaps being depressed below the terminal faces of the last-formed chambers.

REMARKS AND DIFFERENTIATION. This species is morphologically very similar to *Redmondoides medius* (Redmond) in its depressed, slightly concave chamber walls and in the markedly angular junction between them and the terminal faces of the chambers. Its apertural characters are, however, quite distinct from those of *Redmondoides*. *Pseudomarssonella maxima* Redmond differs in possessing a broader umbilical area, with more convex umbilical flaps, in lacking the protrusive mural–septal junctions at the terminal peripheries of the chambers, and in being slightly more slender (tapering at 35°–40°).

Redmond (1965) distinguished *P. reflexa* by its conical test growth, in which the chambers were believed to enlarge more rapidly as ontogeny proceeded, producing an increasing angle of flare in the later test and concave sides to the test as a whole. As only the holotype of this nominal species was deposited by Redmond (there were no paratypes), nothing can be independently and objectively assessed of the constancy of such a morphocharacteristic. However, we can see no difference between this species, as represented by its holotype, and *P. plicata*, and, as first revisers (ICZN Art. 24), we choose the latter to be the senior synonym.

PROVENANCE OF TYPES. The type specimens of *P. plicata* were obtained by Redmond (1965) from Aramco well T 60A (as for *P. maxima*), at 10–20 ft depth, from the basal member of the Upper Dhruma Formation. The type of *P. reflexa* came from Aramco stratigraphic well 4A (27°51′19″N, 44°54′47″E), a core from 4875 ft depth, Middle Dhruma Formation.

STRATIGRAPHY. Redmond (1965) stated that '*P. reflexa* . . . [was] common in the middle part of middle Dhruma', and Powers (1968) recorded it from Dhruma Unit 6 (*Tulites* Zone) and Unit 7 (*Micromphalites* Zone). Enay *et al.* (1987) renamed these units D4 and D5, and referred both to the early Bathonian. In contrast, *P. plicata* was said by Redmond (1965) to be 'common in [the] upper part of [the] basal member of [the] Upper Dhruma Formation', and was reported by Powers (1968) to occur in the 'Atash (chalky) Member, Unit 9, lower part of the Upper Dhruma. Enay *et al.* (1987) called this member 'Unit D7a', but could not determine whether it was of late Bathonian or early Callovian age. Consequently, the known stratigraphical range of this species, as here understood, is from early to late Bathonian and possibly to early Callovian also.

Genus *PARAVALVULINA* Septfontaine, 1988

TYPE SPECIES. *Paravalvulina complicata* Septfontaine, 1988.

DIAGNOSIS EMENDED. A chrysalinid with an initially quadriserial test reducing to adult triseriality; adult primary aperture interiomarginal, umbilical, covered by a broad flap which is penetrated by multiple, areal, accessory pore-like apertures; the apertural flap is convex and is attached to the top of the apertural face of the primary chamber, so that the test is terminally wholly convex; pillars link successive apertural flaps, so that the axial, umbilical part of the test is pillared, throughout its later ontogenetic stages at least; however, the primary chamber lumina, at the equatorial periphery of the test, remain unpillared; wall solid, in early ontogeny at least, sometimes becoming protocanaliculate in late growth stages.

REMARKS. Septfontaine (1988) stated that *Paravalvulina* had three chambers per whorl. However, the published photograph of the equatorial section of *P. complicata* (Septfontaine, 1981: pl. 2, fig. 15; cited under the new name by Septfontaine, 1988: 248) discloses that there can be four chambers per whorl in this species. *P. arabica* (Henson) has the same ontogenetically early quadriseriality (Figs 90, p. 144, & 95, p. 146).

DIFFERENTIATION. *Paravalvulina* is grossly homeomorphic with *Dukhania*, but differs in its quadriserial–triserial growth: megalospheric *Dukhania* is triserial to biserial in ontogeny. Also, the aperture of each chamber in the earliest whorls of *Paravalvulina* possesses a broad, imperforate lip which is depressed relative to the convexity of the true septa (similar to that of the adult, ancestral *Redmondoides*); these lips rapidly become perforated by areal, cribrate accessory apertures (like those of the nearer ancestor *Pseudomarssonella*) but the lips do not achieve a convexity equivalent to that of the true septa until the third or fourth whorl (after the proloculus) is reached. The apertural 'shields' of the adult are still less strongly convex than those of *Dukhania*, in which the terminal convexity of the *Praechrysalidina* ancestral form is displayed.
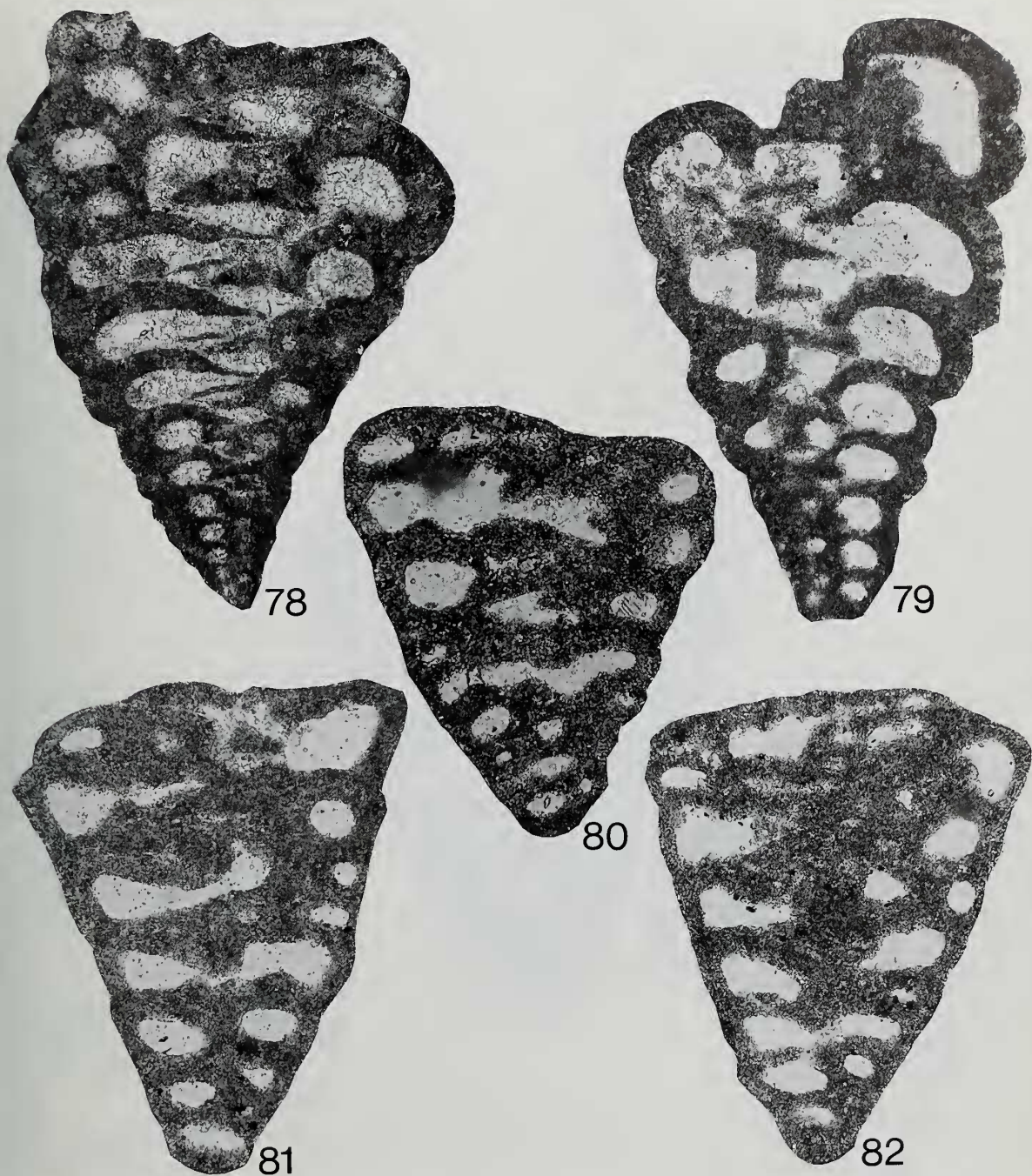
Fig. 78 *Redmondoides lugeoni* (Septfontaine), BMNH P 52621, from United Arab Emirates, off-shore Abu Dhabi, Izhara Formation, probably Bajocian; length 1180 μm, × 80; note protocanaliculation and canaliculation of the walls of late chambers.

Fig. 79 *Redmondoides rotundatus* (Redmond), BMNH P 52622, from off-shore Qatar, Diyab Formation, Oxfordian; length 1080 μm, × 90; note canaliculi in walls of later whorls.

Fig. 80 *Redmondoides* cf. *inflatus* (Redmond), BMNH P 52623, from United Arab Emirates, off-shore Abu Dhabi, Uwainat Formation, probably Bathonian; length 520 μm, × 130.

Fig. 81 *Pseudomarssonella* cf. *plicata* Redmond, BMNH P 52624, from United Arab Emirates, off-shore Abu Dhabi, Uwainat Formation, probably Bathonian; length 620 μm, × 125.

Fig. 82 *Paravalvulina* sp., BMNH P 52625, from United Arab Emirates, off-shore Abu Dhabi, Uwainat Formation, probably Bathonian; length 580 μm, × 130; note the morphologically primitive development of pillars between successive apertural flaps of late ontogenetic stages.

PHYLOGENETIC AFFINITY AND SKELETAL FUNCTION. The initial quadriserial whorls, with their relatively depressed and initially imperforate. flap-like, apertural lips, indicate ancestry in species of *Redmondoides* and *Pseudomarssonella*. Canaliculation of the walls is known in the last-formed chambers of species of both of these genera (e.g., *R. lugeoni, P. maxima*) and it has been reported (as a 'keriotheca') in *Paravalvulina complicata* by Septfontaine (1988). Although protocanaliculation occurs (Fig. 96, p. 146), canaliculi have not yet been observed in specimens of *P. arabica* (Henson). It seems that the development of canaliculi did not continue (or, at least, was not increased) during the course of this evolutionary lineage.

We suggest that the development of multiple, cribrate, accessory, pore-like apertures, in the closely adjacent, successive apertural 'shields', made the development of canaliculi not especially advantageous for the maintenance of adequate communication between intrathalamous cytoplasm and external sea-water; the ion-exchange function of the cytoplasm trapped in the canaliculi could have been replaced by that of the cytoplasm extruded as multiple strands through the accessory apertural, areal pores. Only in the largest specimens, where separation of intrathalamous cytoplasm from sea-water was most complete, would the development of canaliculi have been helpful.

The development of the apertural 'shields' in the umbilical area (with intershield pillars to strengthen the structure and to keep the successive shields spaced apart) could have been for the partial enclosure of umbilical cytoplasm, which has been shown in many Recent rotaline foraminifera (Alexander 1985) to be a reservoir of enzymes for the digestion of disaggregated nutrient particles prior to the ingestion of the nutrients, themselves, into the cytoplasm fully inside the chambers. In such benthic rotalines (e.g. *Haynesina, Rosalina*) partial closure by skeletal material of the umbilical digestive cytoplasm seems to be advantageous, as it serves as a physical division between the truly intrathalamous cytoplasm, the umbilical digestive cytoplasm and the extrusive, pseudopodial cytoplasm. It seems likely that a similar benefit was produced by the test structure in *Paravalvulina*.

The biological advantage which the umbilical structure of Jurassic *Paravalvulina* provided would have been repeated by the development, for the same biological reasons, of similar structures in Cretaceous *Dukhania*. This explains the iterative evolution of these gross homeomorphs.

Paravalvulina arabica (Henson, 1948)   Figs 88–104

1948 *Dukhania arabica* Henson: 616; pl. 15, figs 6, 7; pl. 17, figs 1, 2.
1968 *Urgonina (Parurgonina) (?) arabica* (Henson); Cuvillier, Foury & Pignatti Morano: 154.
1975 *Pseudochrysalidina (?) arabica* (Henson); Schroeder, Geullal & Vila: 324; pl. 2, figs 1, 2.
1976 *Pseudochrysalidina arabica* (Henson); Kalantari: 36–40; pl. 6; pl. 7; pl. 8, fig. 1.

DESCRIPTION EMENDED. Test calcareous, microgranular, with rare to very rare, scattered non-calcareous grains (e.g. quartz); the microgranules of calcite in the walls are either randomly orientated or become linearly orientated, in rows perpendicular to the wall surface, to produce a protocanaliculate structure; canaliculi are not yet known. In thin section, the innermost and outermost surfaces of the walls are optically darker, and these were probably composed of granules significantly smaller, or more densely packed, than those of the main mass of the wall.

The test-form is conical, initially with a broadly acute or slightly obtuse growth angle. The test is initially quadriserial (at least in the megalospheric form) but becomes triserial in later ontogeny. Later chambers do not terminally completely cover earlier ones, but leave the terminal faces of previous chambers partly exposed. The primary aperture of each chamber in the nepionic to ephebic stages is simple, umbilical and interiomarginal, covered by a broad, flap-like lip; in neanic–ephebic growth the flap becomes penetrated by multiple, areal, cribrate, accessory apertural pores; the opening of the primary aperture becomes higher and the flap becomes attached to the highest part of the primary apertural face; the flap becomes a trematophore-like perforate 'shield' (as named by Henson, 1948). All the shields of the last-formed chambers (distinct from the convex terminal faces of the last-formed chambers themselves, which remain exposed) span much or all of the umbilicus and create a slightly, but distinctly, convex termination to the test.

Internally, many pillars are developed, even in the nepionic stage, from the interpore areas of the shields, to reach and fuse with the shields of immediately preceding chambers. The lumina of the chambers themselves, marginal to the shields, lack pillars. In neanic–ephebic growth, the pillars multiply, often crowding together, producing a densely pillared ('labyrinthic') umbilical zone, central to the long axis of the test.

Fig. 83 *Pseudomarssonella* cf. *maxima* Redmond, BMNH P 52626, from United Arab Emirates, off-shore Abu Dhabi, Lower Araej Formation, Bajocian or Bathonian; length 600 µm, × 130.

Fig. 84 *Pseudomarssonella* cf. *bipartita* Redmond, BMNH P 52627, from off-shore Qatar, Uwainat Formation, probably Bathonian; length 1030 µm, × 75.

Fig. 85 'Praechrysalidina' cf. *infracretacea* Luperto Sinni, BMNH P 52628, from United Arab Emirates, subsurface on-shore Abu Dhabi, Mauddud Formation (late Albian–mid Cenomanian); axial section, length 1540 µm, × 65; incomplete pillars between the cribrate, apertural flaps of late whorls herald the evolution of the continuously, completely pillared *Dukhania* (compare Figs 17–19 & 21–26, p. 112–114), and mimic the development of incomplete pillars in the late ontogeny of 'Pseudomarssonella' in its evolution to *Paravalvulina* (see Fig. 86).

Fig. 86 'Pseudomarssonella' cf. *plicata* Redmond (compare Figs 75–77, p. 139), BMNH P 52629, from United Arab Emirates, off-shore Abu Dhabi, Lower Araej Formation, Bajocian or Bathonian; with incomplete pillars between the apertural flaps of the last whorl in the evolution of *Paravalvulina*.

Fig. 87 'Paravalvulina' aff. *complicata* Septfontaine, BMNH P 52630, from United Arab Emirates, off-shore Abu Dhabi. Upper Araej Formation, probably Callovian; length 780 µm, × 125; a few incomplete, and rarer complete, pillars are developed between the apertural flaps.
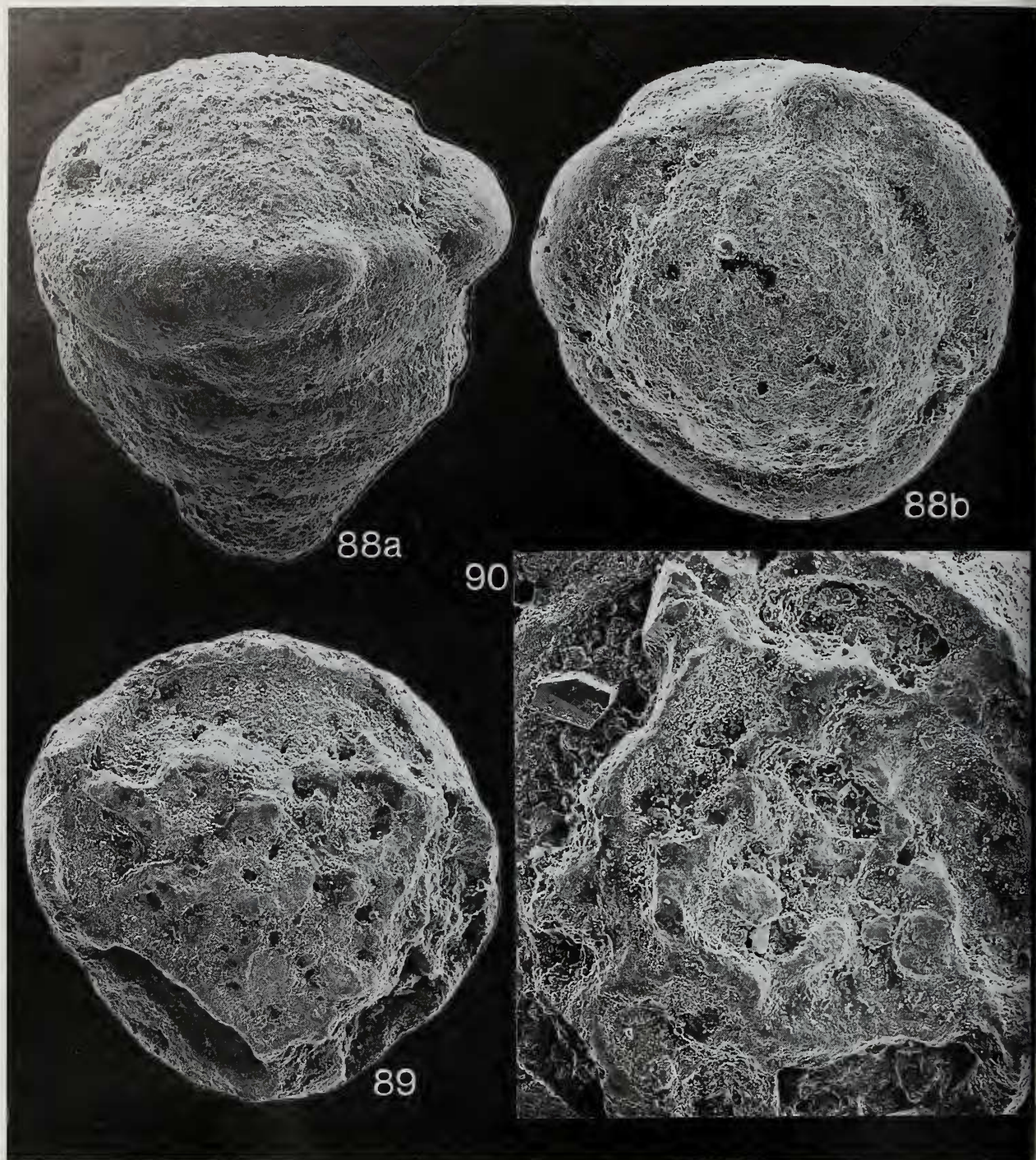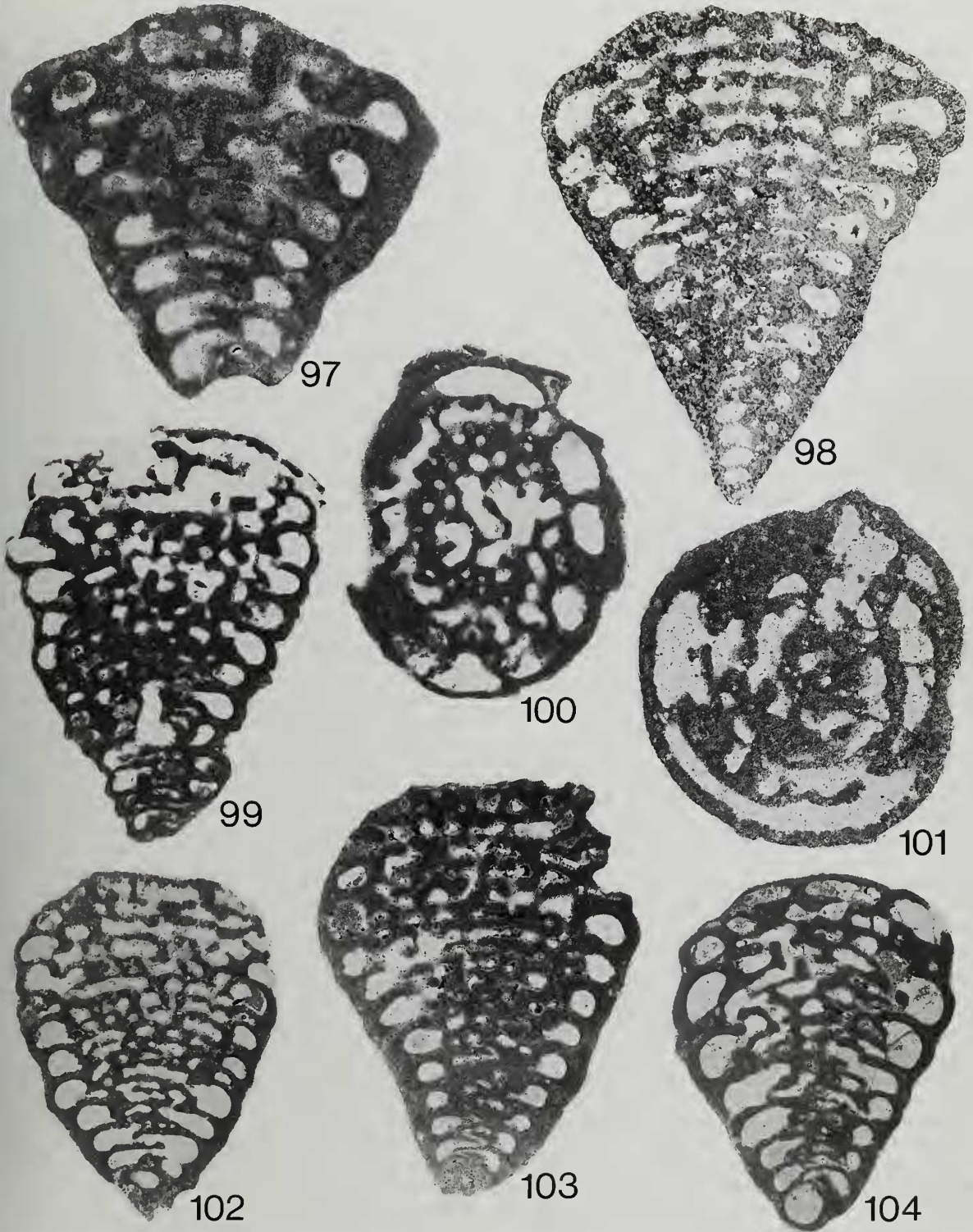
Figs 88–90 *Paravalvulina arabica* (Henson), strictly topotypic paratypes, from Qatar, Well Dukhan-2, 4375–4380 ft depth, Hauterivian. Figs 88a–b, BMNH P 52631, entire specimen; a, axial view (length 1,240 μm), × 70; b, terminal view, × 70. Fig. 89, BMNH P 52632; equatorial view of specimen from which the initial end has been broken, showing initial quadriseriality and umbilical pillars between the cribrate, pore-like apertures of the umbilical, apertural flaps; breadth 1,100 μm, × 70. Fig. 90, BMNH P 52633; initial end of specimen which has lost its chamber walls, showing initial quadriseriality, × 110.

gs 91–94   *Paravalvulina arabica* (Henson); specimens which have lost part or all of their outer chamber walls; from Qatar, Well Dukhan-2, 4375–4380 ft depth, Hauterivian. Fig. 91, BMNH P 52634, terminal view (breadth 1,620 μm), × 50, with umbilical-apertural flap partly broken, showing internal, umbilical pillars. Fig. 92, BMNH P 52635, oblique-axial view (breadth 1,080 μm), × 70, showing umbilical pillars between the cribrate apertural pores in the umbilical-apertural flaps. Fig. 93, BMNH P 52636, axial view (length 1,100 μm), × 80; showing main chambers free of pillars (which fill the inner, umbilical area). Fig. 94, BMNH P 52637, axial view (length 1,580 μm), × 60, of specimen from which the chambers, themselves, have been eroded, leaving only the intensely pillared umbilical regions of successive whorls.
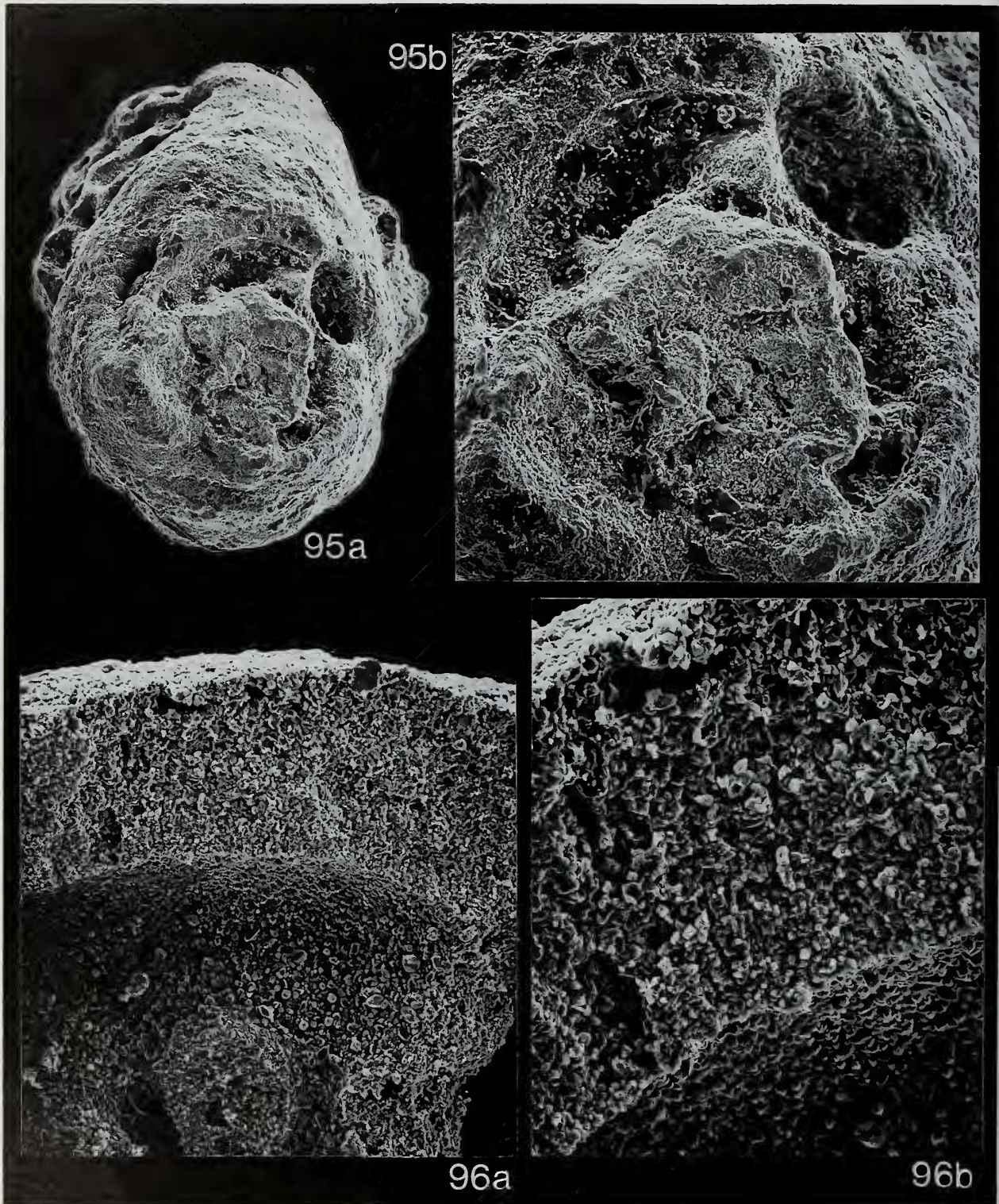
Figs 95–96   *Paravalvulina arabica* (Henson), from Qatar, Well Dukhan-2, 4375–4380 ft depth, Hauterivian. Figs 95a–b, BMNH P 52638; initial view, showing initial quadriseriality; a (breadth 1,200 μm), × 70; b, enlargement of initial whorls, × 150. Figs 96a–b, BMNH P 52639; microgranular, calc-agglutinated wall, broken in cross-section, displaying the shape, size and distribution of the constituent calcareous microgranules; a, broken wall, adjacent interior surface, broken pillar and adjacent pore, × 350; b, enlargement of wall structure, × 800, showing partial linear arrangement of columns of calcareous microgranules (partial protocanaliculation).

Figs 97–104 *Paravalvulina arabica* (Henson). Fig. 97, BMNH P 52640, from Qatar, Well Dukhan-3, 5117–5137 ft depth, Hauterivian; axial section length 820 μm, × 80. Fig. 98, BMNH P 52641, from United Arab Emirates, Well Jumayla-1 (Jamayla-1), 10,041.08 ft depth, Zakum Formation, Valanginian; axial section (length 1,740 μm), × 50. Figs 99–100, paratypes, from Qatar, Well Dukhan-2, 4375–4380 ft depth, originally dated as 'Infravalanginian' but now referred to the Hauterivian. Fig. 99, BMNH P 39108, axial section (length 2240 μm), × 30. Fig. 100, BMNH P 39107, equatorial section (maximum breadth 1780 μm), × 35. Figs 101–104, strict topotypes (locality and depth as for P 39107–8). Fig. 101, BMNH P 52642, equatorial section (maximum breadth 1400 μm), × 40. Fig. 102, BMNH P 52643, axial section (length 1920 μm), × 30. Fig. 103, BMNH P 52644, axial section (length 1960 μm), × 35. Fig. 104, BMNH P 52645, axial section (length 1800 μm), × 35.

DIFFERENTIATION. *Paravalvulina arabica* differs from *P. complicata* Septfontaine in possessing much narrower true chamber lumina and a broader and more densely pillared umbilical zone. The true septa of *P. arabica* are much thinner relative to chamber height, being about 20% of the total chamber height, compared to 35–40% in *P. complicata*.

REMARKS. Although Henson (1948) referred this species to his new genus *Dukhania* without expressing doubts, the specimens which were labelled in the Henson and associates collection (and which are now in the Natural History Museum, London) were only doubtfully assigned to *Dukhania* (i.e., being labelled '*Dukhania? arabica* Henson MS'). This doubt is now explained by the present study and by the revised assignment of the species to the genus *Paravalvulina* Septfontaine. *P. arabica* (Henson) and *Dukhania conica* Henson (p. 111) are phylogenetically distinct, gross homeomorphs.

Cuvillier *et al.* (1968) noted that there were resemblances between *Dukhania arabica* Henson and the newly proposed type species of their new subgenus, *Urgonina (Parurgonina) caelinensis*, so much so that they hesitantly referred Henson's species to that subgenus. However, the adult *Parurgonina* is uniserial, and has been considered by Septfontaine (1988) to be an independent, Oxfordian–'Portlandian' descendant from '*Valvulina lugeoni*' (i.e., from *Redmondoides* sp.). Schroeder *et al.* (1975) photographed axial sections of two topotypes of *Dukhania arabica* (from well Dukhan-2, Qatar, 4375–4380 ft depth), and these, with sections of two other topotypes, failed to show the canaliculate ('keriothecal') walls believed to characterize *Parurgonina caelinensis* (as photographed by Schroeder *et al.*, 1975: pl. 1, fig. 3 and pl. 2, figs 3–5). Nevertheless, protocanaliculation can occur weakly in the walls of *Paravalvulina arabica* (Figs 96–98) and a distinction based solely on such a character must not be expected to be reliable.

STRATIGRAPHY. *P. arabica* was originally obtained by Henson (1948) from limestones and marls (also containing *Pseudocyclammina lituus* (Yokoyama) as described by Banner & Whittaker, 1991) drilled in Qatar (the holotype and paratypes from well Dukhan-2, at 4375–4380 ft depth; other specimens coming from well Dukhan-3, at 5117–5137 ft depth). These beds were once thought to be of 'Infravalanginian' age but are now referred to the Hauterivian (Banner & Whittaker 1991). *Paravalvulina arabica* was also found (and well illustrated) by Kalantari (1976) in the Valanginian–Hauterivian Fahliyan Formation of south-west Iran. These are the youngest known occurrences of *Paravalvulina*. Septfontaine (1988) considered the range of the genus to be that known only for the type species, i.e. 'U. Bajocian (?) to Bathonian', as the type specimens of *P. complicata* were obtained by him from Bathonian limestones of Sardinia. We have found morphologically primitive specimens of *Paravalvulina* sp. in the Uweinat Formation (probably Bathonian), drilled off-shore at Abu Dhabi (Fig. 82, p. 141), and other specimens, here called '*P.*' aff. *complicata*, with more complete inter-flap pillars (Fig. 87), from the Upper Araej Formation (probably Callovian) of the same area. The known and proved biostratigraphic range of the genus is Bathonian to Hauterivian.

CONCLUSIONS

The family Chrysalidinidae contains taxa which are calc-agglutinating, and in which the calcareous microgranules may

align so that their walls become protocanaliculate. True canaliculi develop in the walls of individuals of many taxa, but at differing stages of growth. No stratigraphically significant, phylogenetic sequence of development from randomly to protocanaliculately orientated microgranules, or from proto-canaliculate to canaliculate wall structure, can be perceived in the Chrysalidinidae. Consequently, it is believed that chrysalidine taxa, at specific or higher categories, cannot be distinguished on these criteria. This conclusion differs from that which may be applicable to other family-groups (e.g., the Eggerellidae, Textulariidae, Valvulinidae, Verneuilinidae, etc.), but it exemplifies the rule that morphological characters have differing degrees of taxonomic importance in different supraspecific taxa. For example, the presence or absence of costae may not even distinguish species in many genera of the Nodosariacea, but they would characterize species in the Heterohelicacea and genera in the Globotruncanacea. The Foraminiferida are too diverse to be governed by simple rules of universal, unchangeable regulation.

Like all other foraminiferid skeletal structures, the wall-structures of the Chrysalidinidae almost certainly had a biological function; it is possible (even probable) that canaliculi had the same function as that possessed by the narrow hypodermal alveoli of some Cyclamminidae (Loftusiacea), and allowed ionic exchange between intrathalamous cytoplasm and external sea-water. In the Chrysalidinidae, this may have become advantageous in different stages of ephebic growth under different environmental conditions, and was not developed if it was not useful. It certainly does not apppear to have been a standard development, as it was in other foraminiferid families.

The Chrysalidinidae are morphologically and phylogenetically divisible into the neanically quadriserial, almost wholly Jurassic Paravalvulininae, and the neanically triserial, Cretaceous Chrysalidininae. These two subfamilies are believed to have had different evolutionary origins, and different detailed patterns of evolution, but both were Tethyan, both were calc-agglutinating with similar histories of canaliculation, and both evolved pillared forms which were closely homeomorphic (*Paravalvulina* and *Dukhania*). In any system of classification, it would seem sensible, practicable and useful to keep these particular genera distinct but close together.

Even with an amalgamation of the Redmond Arabian collection, the Henson and associates collection from Iraq, Iran and Qatar, and additional material from the United Arab Emirates, Oman and elsewhere, we still do not know the ancestor of the earliest known Paravalvulininae. The oldest known genera (*Riyadhella* and *Redmondoides*) both appear in the Late Bajocian (Fig. 105). Species of the former occur in beds at least as young as Oxfordian, while species of the latter are known from beds as young as Kimmeridgian. Stratigraphically late species, at least, of both genera (*Riyadhella inflata*, *Redmondoides inflatus*) spread into more northerly areas, while at least one of the latter (*Redmondoides lugeoni*) became widespread throughout Tethys. Another, stratigraphically early and morphologically simple, genus (*Riyadhoides*) was short-lived (Bajocian) and apparently confined to central Tethys. The development of cribrate apertures in non-pillared forms (species of *Pseudomarssonella*) appears to have been confined to the Bathonian and Callovian, but umbilical pillaring developed rapidly – it is recorded (as *Paravalvulina*, by Septfontaine, 1988) also from the Bathonian of Tethys. The evolution of pillared forms
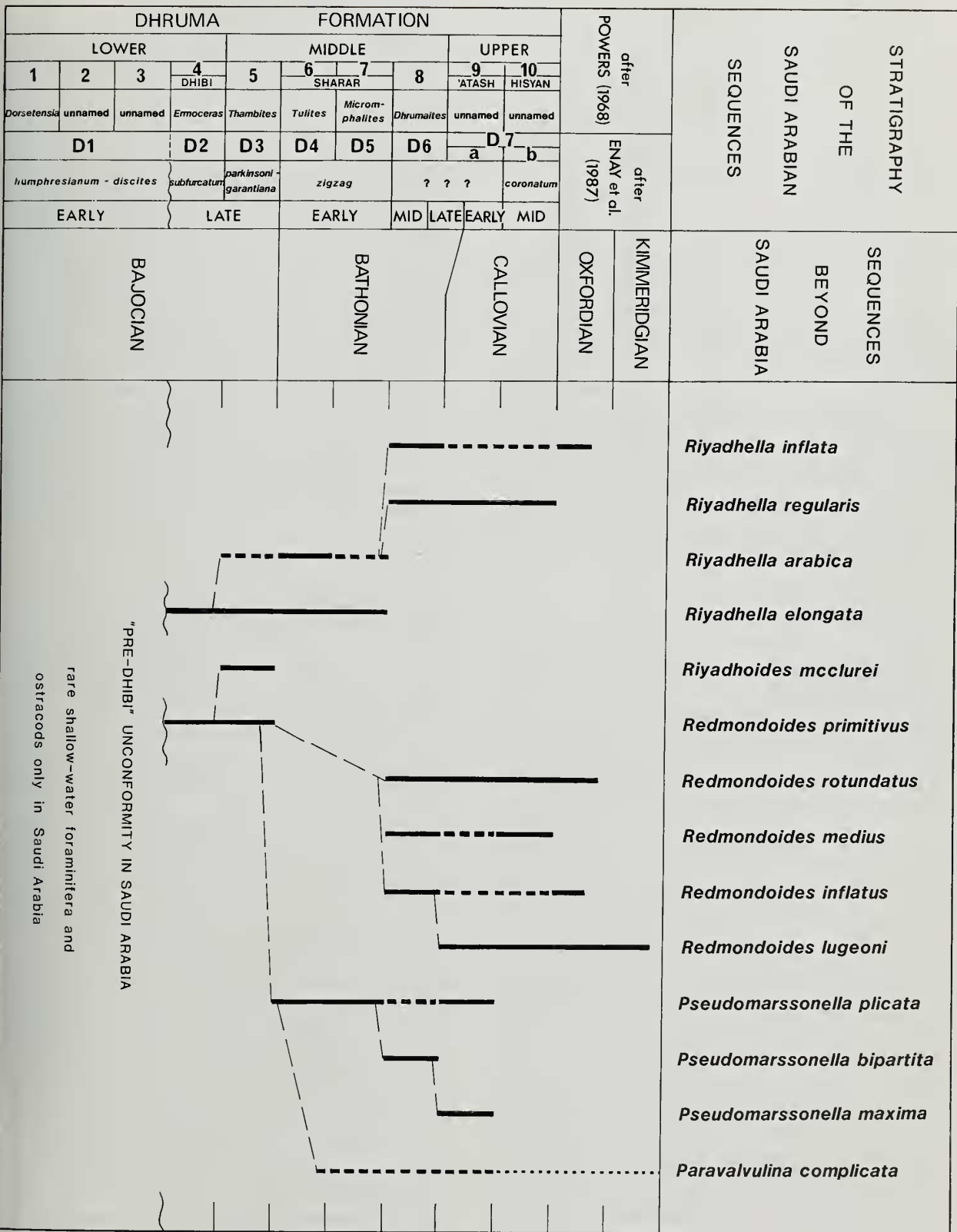
Fig. 105 Stratigraphical ranges of the Jurassic Paravalvulininae. Continuous lines represent firmly known occurrences, dashed lines represent doubtfully dated occurrences or stratigraphically intermediate intervals, while the dotted line (*Paravalvulina complicata*) links to the early Cretaceous occurrence of the last member of this subfamily, *P. arabica*.
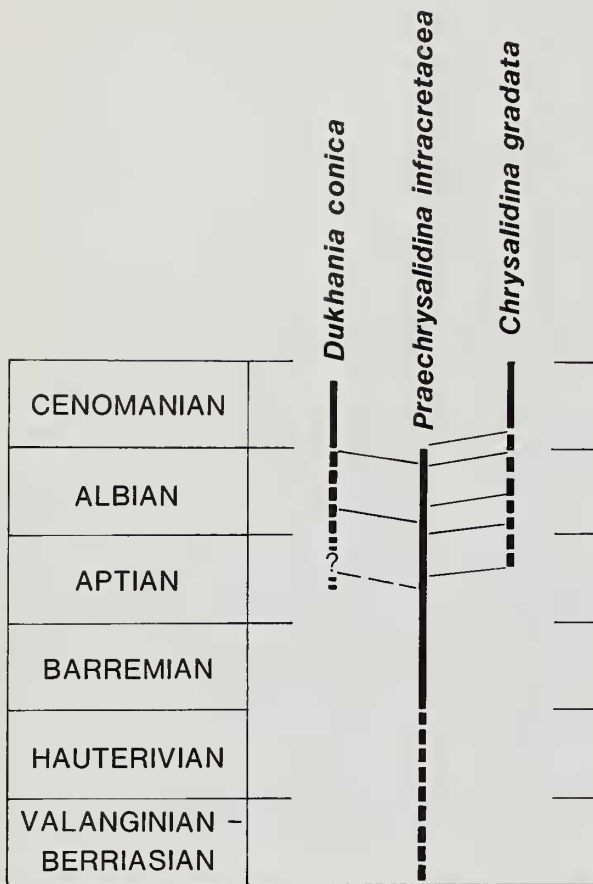
Fig. 106 Stratigraphical ranges of the early to mid-Cretaceous taxa of the Chrysalidininae; dashed lines represent the occurrences of ancestral, morphologically primitive forms, while continuous lines represent the occurrence of typical forms of the named species.

seems to have been gradual, as morphologically simple forms (e.g., Figs 85, 86, p. 142) are known from beds probably as young as Callovian. *Paravalvulina arabica*, also from Tethys, occurred in the earliest Cretaceous, and was the last of the Paravalvulininae.

The Chrysalidininae (Fig. 106) seem to have evolved independently and directly from *Verneuilinoides* in the earliest Cretaceous, by the appearance of the unpillared *Praechrysalidina*. The development of pillars (in the late Aptian–Albian) was gradual, producing gross homeomorphs of the antecedents of true *Paravalvulina* (e.g., Fig. 85; compare Figs 86 and 87), and completely pillared forms were clearly developed in the Cenomanian. These included the rapidly tapering, terminally biserial *Dukhania* and the slowly tapering, terminally triserial *Chrysalidina*. Although both were of Cenomanian age, they appear to have developed independently from *Praechrysalidina*: the former seems to have been confined to central Tethys, and to have had no descendants, while the latter spread throughout western and central Tethys (at least from western France to Yemen and Oman) and probably gave rise to *Accordiella* in the Coniacian–Campanian.

The reillustration of all the above-mentioned taxa (except *Accordiella*), whenever possible both by the SEM of solid

specimens and by the optical photography of their thin sections, has made possible their umambiguous reidentification, and, consequently, their limited stratigraphical ranges have proved their potential use in the biostratigraphy of the mid Jurassic – late Cretaceous neritic marine sediments of, at least, central and western Tethys.

REFERENCES

Alexander, S. P. (1985). *The cytology of certain benthonic foraminifera in relation to test structure and function.* Univ. Wales, Univ. coll. Swansea, unpublished Ph.D. thesis.

Azzaroli, A. & Reichel, M. 1965. Alveoline e Crisalidine Neocretacee del 'Calcare di Mola' in Terra di Bari. *Bollettino di Servizio Geologico d'Italia*, Rome, **85**: 3–9, pl. 1.

Banner, F. T. & Desai, D. 1985. The genus *Clavulinoides* Cushman emended and the new Cretaceous genus *Clavulinopsis*. *Journal of Foraminiferal Research*, Washington, **15**: 79–90, pls 1–4.

—— & Pereira, C. P. G. 1981. Some biserial and triserial agglutinated smaller foraminifera: their wall structure and its significance. *Journal of Foraminiferal Research*, Washington, **11**: 85–117, pls 1–10.

—— & Whittaker, J. E. 1991. Redmond's 'New Lituolid Foraminifera' from the Mesozoic of Saudi Arabia. *Micropaleontology*, New York, **37**: 41–59, pls 1–6.

Baud, A., Heinz, R. & Septfontaine, M. 1989. Compte rendu de l'excursion de la Société Géologique Suisse dans les Préalpes, du 2 au 4 Octobre 1988. *Eclogae Geologicae Helvetiae*, Basel, **82**: 359–377.

Bayliss, D. D. 1966. Foraminifera from the Bau Limestone Formation, Sarawak, Malaysia. *Report of the Geological Survey, Borneo Region, Malaysia*, Kuching, **1965**: 173–195, pls 51–52.

Bender, H. 1989. Gehäuseaufbau, Gehäusegenese und Biologie agglutinierte Foraminiferen (Sarcodina, Textulariina). *Jahrbuch der Geologischen Bundesanstalt*, Vienna, **132**: 259–347, pls 1–17.

—— & Hemleben, C. 1988. Calcitic cement secreted by agglutinated foraminifers grown in laboratory culture. *Journal of Foraminiferal Research*, Washington, **18**: 42–45, pl. 1.

Brun, L. 1963 (1962). La repartition stratigraphique des *Pseudocyclammina lituus* (Yokoyama) dans le sud-ouest Marocain. *Notes et Mémoires du Service Géologique du Maroc*, Rabat, **156** (21, Micropaléontologie): 93–98, pls 1–2.

Castro, P. de 1981. Osservazioni su *Chrysalidina gradata* d'Orbigny 1839 (*Foraminiferida*) dell'Île Madame (Francia). *Atti dell'Accademia Pontaniana*, Naples, (n.s.) **30**: 1–25, pls 1–8.

Cole, W. S. 1941. Stratigraphy and micropaleontology of two deep wells in Florida. *Geological Bulletin, Florida State Geological Survey*, Tallahassee, **16**: 1–73.

Cuvillier, J., Foury, G. & Pignatti Morano, R. 1968. Foraminifères nouveaux du Jurassique supérieur du Val Cellina (Frioul occidental, Italie). *Geologica Romana*, **7**: 141–156, pls 1–2.

Delage, Y. & Hérouard, E. 1896. La cellule et les protozoaires. *Traité de Zoologie Concrète*, 1. 584 pp. Paris.

Delance, J. H. & Ruget, C. 1989. Foraminifères du Dogger Nivernais. *Revue de Micropaléontologie*, Paris, **32**: 195–214, pls 1–4.

Desai, D. & Banner, F. T. 1987. The evolution of Early Cretaceous Dorothiinae (Foraminifera). *Journal of Micropalaeontology*, London, **6** (2): 13–27, pls 1–5.

Dunnington, H. V., Wetzel, R. & Morton, D. M. 1959. Mesozoic and Palaeozoic. *Lexique Stratigraphique Internationale*, 3 *Asie:* (10a, Iraq). 333 pp. Paris (CNRS).

Enay, R., Le Nindre, Y. M., Mangold, C., Manivit, J. & Vaslet, D. 1987. Le Jurassique d'Arabie saoudite centrale: nouvelles données sur la lithostratigraphie, les paléoenvironnements, les faunes d'Ammonites, les âges et les correlations. *Geobios*, Lyon, Mém. Spec. 9: 13–66.

Farinacci, A. 1962. Nuovo genere di Verneuilinidae (Foraminifera) marker di zona del Senoniano. *Geologica Romana*, 1: 5–10, pls 1–5.

Furrer, U. & Septfontaine, M. 1977. Nouvelles données biostratigraphiques (à l'aide des Foraminifères) dans le Dogger à faciès briançonnais des Préalpes médianes romandes (Suisse). *Eclogae Geologicae Helvetiae*, Basel, **70**: 717–737.

Gušić, I. 1975. Lower Cretaceous imperforate Foraminiferida of Mt. Medvednica, northern Croatia (Families: Lituolidae, Ataxophragmiidae, Orbitolinidae). *Palaeontologia Jugoslavica*, Zagreb, **14**: 1–51, pls 1–31.

Haeusler, R. 1890. Monographie der Foraminiferen-fauna der Schweizerischen Transversarius-zone. *Abhandlungen der Schweizerischen Paläontologischen Gesellschaft*, Zurich, **17**: 1–134, pls 1–15.

Hamaoui, M. & Saint-Marc, P. 1970. Microfaunes et microfaciès du Cénomanien du Proche-Orient. *Bulletin du Centre de Recherches de Pau. Société Nationale des Pétroles d'Aquitaine*, **4**: 257–352, pls 1–40.

Henson, F. R. S. 1948 (1947). New Trochamminidae and Verneuilinidae from the Middle East. *Annals and Magazine of Natural History*, London, (11) **14**: 605–630, pls 14–18.

—— 1949. Recent Publications on Larger Imperforate Foraminifera of the Middle East. *Annals and Magazine of Natural History*, London, (12) **2**: 173–177.

Hofker, J. 1966. Maestrichtian, Danian and Palaeocene Foraminifera. The foraminifera of the type-Maestrichtian in south Limburg, Netherlands, together with the foraminifera of the underlying Gulpen Chalk and the overlying calcareous sediments; the foraminifera of the Danske Kalk and the overlying greensands and clays as found in Denmark. *Palaeontographica*, Stuttgart, Supplement Bd **10**: 1–375.

Hottinger, L. 1967. Foraminifères imperforés du Mésozoïque marocain. *Notes et Mémoires du Service Géologique du Maroc*, Rabat, **209**: 1–169, pls 1–20.

——, Halicz, E. & Reiss, Z. 1990. Wall texture of *Spirorutilus*. *Journal of Foraminiferal Research*, Washington, **20**: 65–70, pl. 1.

Kalantari, A. 1976. Microbiostratigraphy of the Sarvestan area, south-western Iran. *Publications, National Iranian Oil Company, Geological Laboratories*, Tehran, **5**: 1–128, pls 1–52.

Levina, V. I. 1972. Podsemeistvo Globotextulariinae [In Dain, L. G., ed., Foraminiferi Verkhneyurskikh Otlozhenii Zapadnoi Sibiri]. *Trudȳ Vsesoyuznogo Neftyanogo Nauchno-Issledovatel'skogo Geologo-Razvedochnogo Instituta (VNIGRI)*, Leningrad, **317**: 100–105, pls 30–32.

Loeblich, A. R. jr & Tappan, H. 1964. Protista 2. Sarcodina, chiefly 'Thecamoebians' and Foraminiferida. In: Moore, R. C. (ed.), *Treatise on Invertebrate Paleontology*, **C**. 1: C1–C510a, text-figs 1–399; 2: C511–C900, text-figs 400–653. Lawrence, Kansas.

—— —— 1988. *Foraminiferal genera and their classification*. 1, 970 pp.; 2, 212 pp., 847 pls. New York.

—— —— 1989. Implications of wall composition and structure in agglutinated foraminifers. *Journal of Paleontology*, Ithaca, NY, **63**: 769–777.

Luperto Sinni, E. 1979. *Praechrysalidina infracretacea* n. gen., n. sp., (Foraminiferida), del Cretaceo Inferiore delle Murge Baresi. *Studi Geologici e Morfologici sulla Regione Pugliese*, Bari, **5**. 16 pp., 3 pls. (Istituto di Geologia e Paleontologia. Università degli Studi di Bari.)

Neumann, M. 1967. *Manuel de Micropaléontologie des Foraminifères (Systématique – Stratigraphie)*. 297 pp., 60 pls. Paris.

Orbigny, A. d' 1839. Foraminifères. In: de la Sagra, R., *Histoire physique, politique et naturelle de l'Île de Cuba*. 1, 224 pp.; 2, 12 pls. Paris.

—— 1846. *Foraminifères fossiles du Bassin Tertiare de Vienne (Autriche)*. xxxvii + 312 pp, 21 pls. Paris.

Parker, W. K. & Jones, T. R. 1865. On some foraminifera from the North Atlantic and Arctic Oceans, including Davis Straits and Baffin's Bay. *Philosophical Transactions of the Royal Society of London*, **155**: 325–441, pls 13–19.

Pelissié, T., Peybernès, B. & Rey, J. 1984. The larger benthic foraminifera from the Middle/Upper Jurassic of SW France (Aquitaine, Causses, Pyrenees). In Oertli, H. J. (ed.), *Benthos '83. 2nd International Symposium on Benthic Foraminifera (Pau, April 1983)*: 479–489. Pau & Bordeaux.

Powers, R. W. 1968. *Lexique Stratigraphique Internationale*, 3 *Asie:* (10b 1, Saudi Arabia (excluding Arabian Shield). 177 pp. Paris (CNRS).

Redmond, C. D. 1965. Three new genera of foraminifera from the Jurassic of Saudi Arabia. *Micropaleontology*, New York, **11**: 133–140.

Riegraf, W. & Luterbacher, H. 1989. Oberjura-Foraminiferen aus dem Nord- und Südatlantik (Deep Sea Drilling Project Leg 1-79). *Geologische Rundschau*, Stuttgart, **78** (3): 999–1045, pls 1–4.

Sartorio, D. & Venturini, S. 1988. *Southern Tethys Biofacies*. 235 pp. Milan.

Schroeder, R., Geullal, S. & Vila, J.-M. 1975. *Parurgonina caelinensis* Cuvillier, Foury & Pignatti Morano, 1968 dans le Malm du Djebel Téioualt (Constantinois, Algérie). *Eclogae Geologicae Helvetiae*, Basel, **68**: 319–326, pls 1–2.

—— & Neumann, M. 1985. Les grands foraminifères du Crétacé Moyen de la région Méditerranénne. *Géobios*, Lyon, Mém. Spec. 7: 1–160, pls 1–68.

Septfontaine, M. 1977. Niveaux à Foraminifères (Pfenderininae et Valvulininae) dans le Dogger des Préalpes médianes du Chablais occidental (Haute-Savoie, France). *Eclogae Geologicae Helvetiae*, Basel, **70**: 599–635, pls 1–2.

—— 1981. Les Foraminifères imperforés des milieux de Plate-forme au Mésozoïque: déterminations pratique, interprétation phylogénétique et utilisation biostratigraphique. *Revue de Micropaléontologie*, Paris, **23**: 169–203, pls 1–3.

—— 1988. Towards an evolutionary classification of Jurassic lituolids (Foraminifera) in carbonate platform environment. *Revue de Paléobiologie*, Geneva, **vol. spéc. 2**, 'Benthos '86': 229–256, pls 1–2.

Simmons, M. D. & Hart, M. B. 1987. The biostratigraphy and microfacies of the early to mid-Cretaceous carbonates of Wadi Mi'aidin, Central Oman Mountains. In Hart, M.B. (ed.), *Micropalaeontology of Carbonate Environments*: 176–207. Chichester.

Smith, A. B., Simmons, M. D. & Racey, A. 1990. Cenomanian echinoids, larger foraminifera and calcareous algae from the Natih Formation, central Oman Mountains. *Cretaceous Research*, London, **11**: 29–69.

SYSTEMATIC INDEX

New taxonomic names and page numbers of the principal references are printed in bold type. Asterisks denote illustrations.